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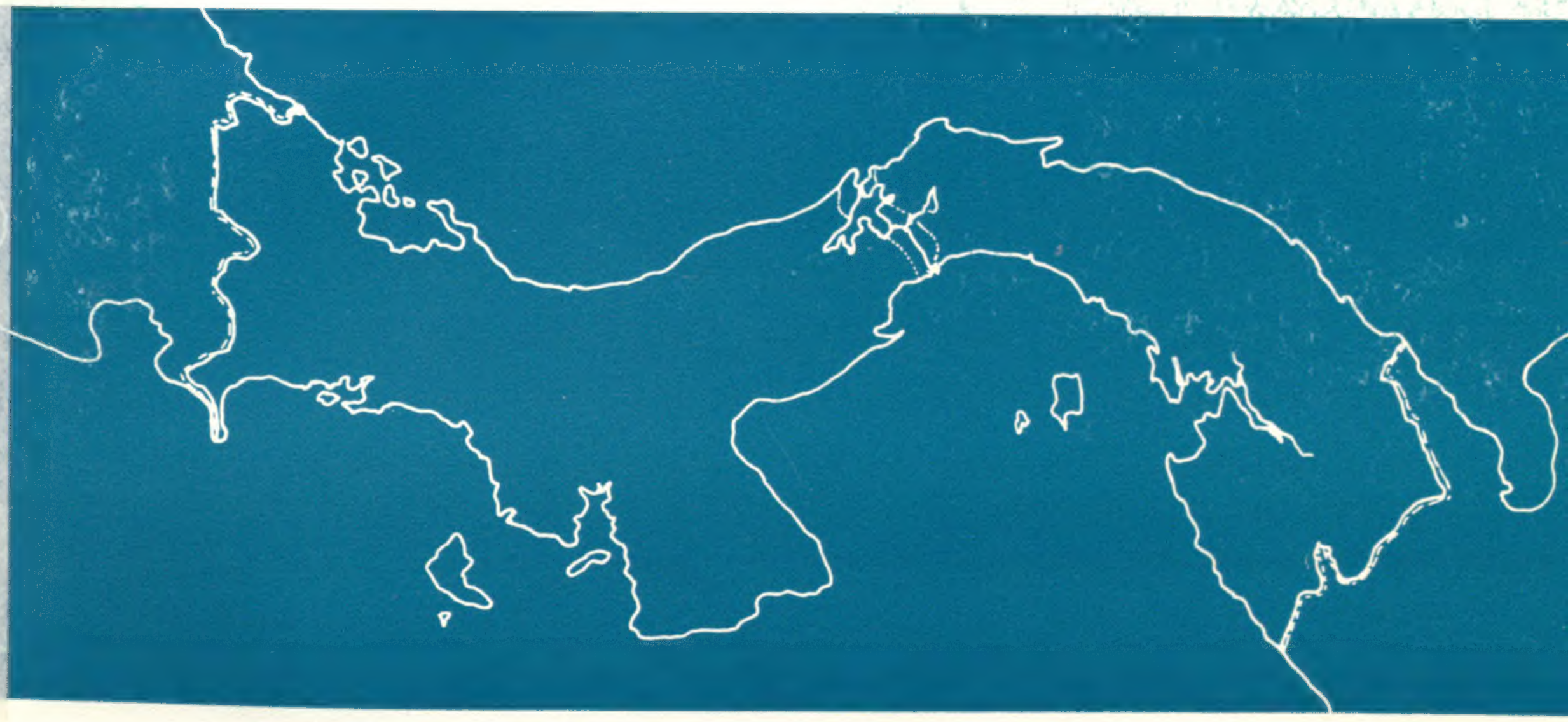

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ANNALS OF THE
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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part II

FAMILY 2A. GNETACEAE[1]

THOMAS B. CROAT[2]

Glabrous trees or shrubs, but chiefly *lianas*. *Leaves* opposite, decussate, simple, estipulate, evergreens, leathery, penninerved. *Inflorescences*[3] branched or simple, dioecious, each segment subtended by 2 opposite, decussate bracts. *Flowers* minute, sessile, arranged in a series of whorls on the stobilus axis, interspersed with numerous moniliform trichomes, the whorls usually subtended by a circular bract or collar, the male spike with the uppermost ring containing usually imperfect female fllowers. *Male flowers* numerous, the perianth tubular, splitting transversely to allow growth of the central stamen; microsporangia 1–2, dehiscing by apical slits. *Female flowers* 3–8 per whorl with a fleshy outer envelope (perianth) surrounding a single orthotropous ovule and two integuments. *Seed* drupe-like, pink, red or yellow.

A family of one genus containing 30 species, confined to the tropical and humid regions of the world.

1. GNETUM

Gnetum L., Mant. Pl. 1: 18. 1767.

Characters of the family.

The genus contains only one little-known taxon in Panama.

---

[1]Assisted by National Science Foundation Grant GB-5674.

[2]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

[3]Because of the highly advanced nature of the family and the difficulty of comparing it with other gymnosperms, I have followed the lead of most authors, who have used such terms as inflorescence, flowers, stamens, etc., for the Gnetaceae, though perhaps in the strictest sense these terms can be attributed only to the angiosperms.

Gnetum leyboldii Tul. var. **woodsonianum** Markgraf, Ann. Missouri Bot. Gard. 52: 385. 1965.—Fig. 1.

Large glabrous, woody, dioeceous *vines*, highly ramified, contorted, and widely climbing to more than 30 m; trunk to 15–20 cm thick near the ground, coarse, but not fissured; branches terete, smooth, nodes enlarged, internodes 3–7 cm long on ultimate branches. *Leaves* opposite, decussate, coriaceous, broadly ovate, acute to short-acuminate, 9–15 cm long and (5–)6–10 cm wide, light green, sometimes shiny, especially above; midrib forming an arch, the apex curved sharply downward, both sides of the blade turned upward with respect to the midrib; veins ± prominent below, obscure above; primary veins usually fewer than 6, forming an obscure collecting nerve distant from the margin; tertiary veins densely anastomosing; leaf margin entire, whitish and incurled on the lower surface; petiole ca. 1 cm long, canaliculate. *Male inflorescence* axillary and terminal, once to twice branched, the main axis consisting of 1–4 tiers, each 1–4 cm long and terminated by 2 small, opposite, acute, connate bracts subtending a dense cluster of moniliform trichomes, a whorl of 2–9 simple, pedicellate strobili, and the axis of the next higher tier; side branches of 1–2 tiers identical to those of the main axis; male strobili greenish-brown, 10–18 mm long and 3 mm wide at maturity, stalks slender, 5–10 mm long; apical portion usually sterile. *Male flowers* numerous, in 6–7 whorls, 1–2.5 mm apart (uppermost whorl with a few, usually sterile female flowers), interspersed in a dense mat of white moniliform trichomes, each whorl subtended by a collar of circular bracts, these at first cup-shaped, becoming saucer-shaped at maturity; male perianth obconic, brownish, angulate, 0.8 mm long and 0.3 mm wide; stamen single, 1.2 mm long, with 2 unilocular microsporangia, moniliform trichomes 1.5–1.8 mm long; external involucre of sterile female flowers (uppermost whorl only) clavate, 0.7 mm long and 0.3 mm wide, the internal involucre short. *Female inflorescence* smaller and more reduced than the male; strobili simple or once branched, the main axis of 3–5 tiers, each terminated by 2 opposite, acute, connate bracts subtending the axis of the next higher tier as well as a whorl of 5 female flowers imbedded in a dense cluster of moniliform trichomes. (Female flowers do not develop on those nodes of the inflorescence where branching occurs.) *Female flowers* brownish-yellow, subglobose, 0.5 mm wide and high, each with a single ovule; 2–3 enlarging ovules appear over the edge of the bracts as the internodes elongate in succession from the lowermost upward (most ovules soon aborting); fruiting internodes 15 mm long and 2 mm thick. Mature *seed* 4.5–5.0 cm long and 2 cm wide, oblong, the margins parallel, the ends both rounded with a minute apical apiculum; external envelope reddish, moderately fleshy, 1 mm thick, smooth, external integument ribbed, the inner integument silky and thin with a long integumentary tube.

Lowland forests of Panama and northern Colombia. (Incorrectly reported by Markgraf (Ann. Missouri Bot. Gard. 52:386. 1965) to range as far as southwestern Colombia.)

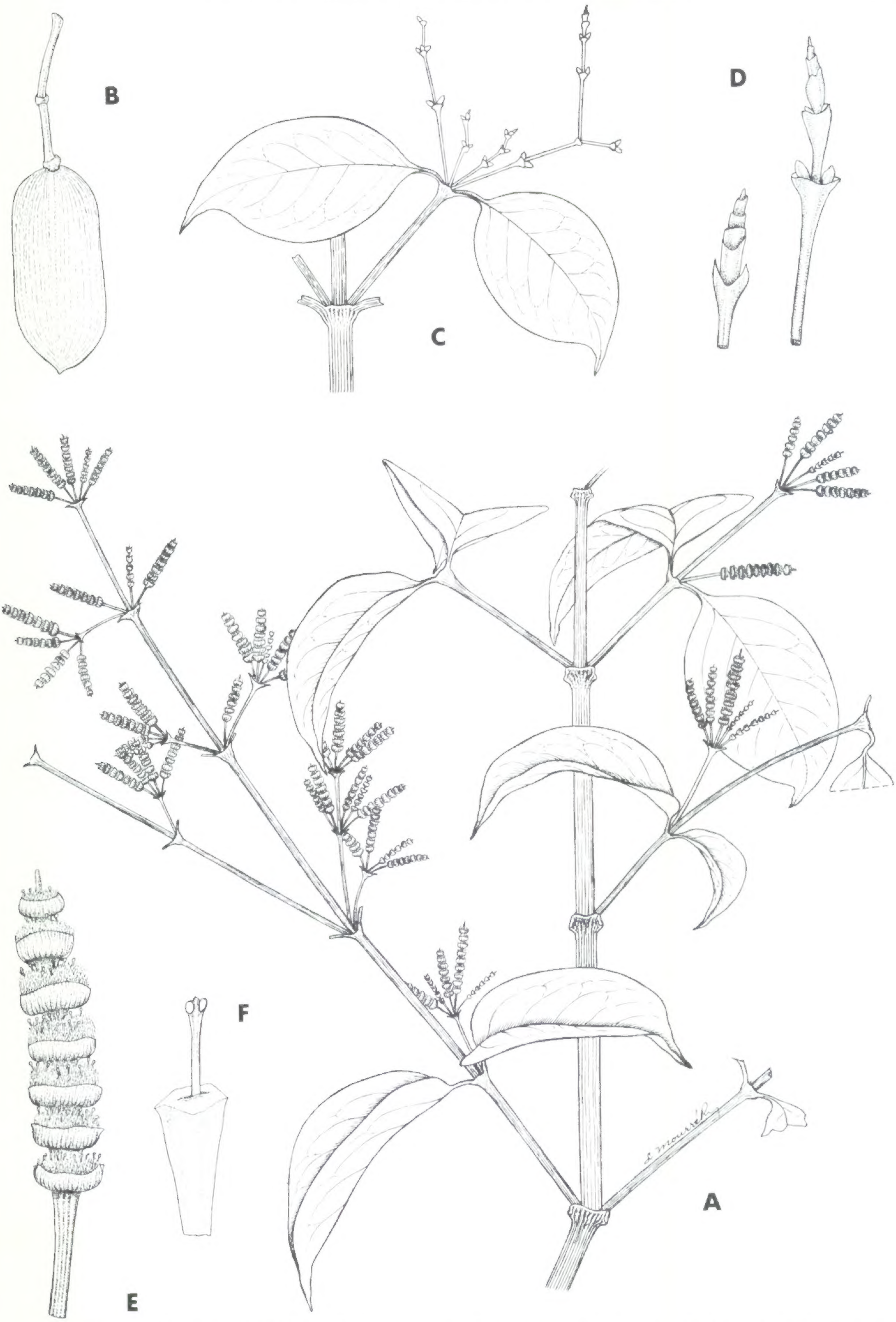

FIGURE 1. *Gnetum leyboldii* Tul. var. *woodsonianum* Mgf.—A. Habit of male plant (× 5/8).—B. Fruit (× 5/8).—C. Habit of female plant (× 5/8).—D. Immature female strobili (× 5).—E. Male strobilus (× 2½).—F. Staminate flower (× 27). [After *Croat* 7958 (MO).]

CANAL ZONE: Barro Colorado Island, Barbour Lathrop Trail 430, *Croat* 7958 (MO); Miller Trail, *Kenoyer* 634 (US); Shoreline of Gigante Bay, *Shattuck 1120* (MO). Vicinity of Gatun Locks & Lake, I.W.T.C. Headquarters, *Johnston 1786* (MO, holotype).

COCLE: Bismarck, above Penonomé, alt. 20 m, *Williams* 608 (US).

DARIEN: Boca de Pauarandó, on Río Sambú, alt. 20 m, *Pittier* 5685 (US). Cerro Pirre, *Bristan* 558 (MO). Vicinity of La Palma, alt. 0–50 m, *Pittier* 5488 (US). Río Pirre, *Bristan 1476* (MO).

While many species of *Gnetum* have male and female inflorescences which are very similar, the type of strobilus found on the male plants of *G. leyboldii* var. *woodsoniana* is probably not common to the female plant.[4] The female inflorescence of this variety apparently represents a considerable reduction from that of the male inflorescence. Both contain short sections of stem topped by a dense cluster of moniliform trichomes subtended by two opposite connate bracts. The female flowers are situated within these trichomes in a ring around the main axis, and it is here that any branching occurs in the female inflorescence. It is doubtful, however, that any fertile male flowers occur at a comparable point on the male inflorescence. Rather it is from these points that the male inflorescence becomes more compound. Either there is a whorl of pedicellate strobili, or both a whorl of strobili and a continuation of the main axis. Branches of the inflorescence also occur at these points.

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

Gnetaceae **1**
Gnetum **1**, 4†
leyboldii
—var. woodsonianum **2**, 4†

[4]The holotype of *G. leyboldii* Tul. var. *woodsonianum* Mgf. contains one loose male strobilus. It is not known whether this was a part of the female plant, thus representing a breakdown of the weak dioecious character of the genus, or if this was originally part of another plant.

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 91. BURSERACEAE[1]

DUNCAN M. PORTER[2]

Trees or shrubs, resin ducts present in the inner bark. *Leaves* alternate, usually odd-pinnate, deciduous or persistent; stipules usually absent. *Inflorescences* axillary to rarely terminal cymose panicles or racemes; plants mostly dioecious. *Flowers* small, regular, hypogynous, 3–5-merous, usually functionally unisexual; sepals 3–5, connate at least basally, imbricate or valvate, persistent; petals 3–5, free or rarely connate into a tube, imbricate or valvate; stamens 6–10, in 1–2 whorls, usually sterile in carpellate flowers, the filaments usually free, inserted below or rarely on the disc, the anthers 2-loculed, versatile, introrse, longitudinally dehiscent; disc intrastaminal or rarely extrastaminal, nectariferous; gynoecium 2–5-carpelled, syncarpous, the ovary 2–5-lobed and -loculed, usually rudimentary in staminate flowers, the ovules 2 per locule, anatropous, epitropous, placentation axile, the style 1, usually short, the stigma 2–5-lobed. *Fruits* more or less drupaceous, the pericarp coriaceous to fleshy, ultimately dehiscent by 2–5 valves; pyrenes 1–5, usually 1-seeded; endosperm absent, the embryo usually straight, the cotyledons contortuplicate or flat, usually lobed, the radicle superior.

A family of about 20 genera and 600 species, reaching its greatest development in tropical America, Malaysia, and northwestern Africa. Four genera are known from Panama. Also to be expected from Darién is the genus *Dacryodes* Vahl, the American species of which have been revised by Cuatrecasas (Trop. Woods 106: 46–65. 1957). The evergreen trees of this genus have unisexual 3-merous flowers with 3 connate sepals, 3 free petals, 6 stamens with connivent anthers, and a 2–3-loculed ovary; the fruit is drupaceous, with a single large pyrene, it is "oblong-ovoid or ellipsoid, with a glabrous, carnose, corrugate pericarp when dry, with a rather thin corneous or cartilaginous endocarp, apical stigma and digitate and folded cotyledons" (Cuatrecasas, op. cit., p. 47).

Bark, leaves, and fruits of all members of the family contain fragrant resins that lead many collectors to comment upon the turpentine-like odors of their specimens.

Useful references:

Brizicky, G. K. The genera of *Simaroubaceae* and *Burseraceae* in the Southeastern United States. Jour. Arnold Arbor. 43: 173–186. 1962.

---

[1]Assisted by National Science Foundation Grant No. GB-5674.

[2]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Cuatrecasas, J. Prima flora colombiana. I. *Burseraceae.* Webbia 12: 375–441. 1957.

Swart, J. J. A monograph of the genus *Protium* and some allied genera. Rec. Trav. Bot. Néerl. 39: 211–446. 1942.

a. Petals free.
  b. Ovary 2–3-lobed and -loculed, the stigma 2–3-lobed; pyrenes 1 (rarely 2) per fruit on the same plant . . . . . 1. *Bursera*
  bb. Ovary 4–5-lobed and -loculed, the stigma 4 5-lobed; pyrenes 1–2(–5) per fruit on the same plant . . . . . 2. *Protium*
aa. Petals connate below to form a tube.
  c. Sepals and petals 4–5 . . . . . 3. *Tetragastris*
  cc. Sepals and petals 3 . . . . . 4. *Trattinnickia*

1. BURSERA

Bursera Jacq. *ex* L., Sp. Pl. ed. 2. 471. 1762, *nom. cons.*

Terebinthus P. Br., Civ. Nat. Hist. Jamaica 345. 1756, non *Terebinthus* P. Mill., Gard. Dict. Abr. ed. 4. 1754.
Simaruba Boehmer *in* Ludwig, Def. Gen. Pl. ed. 3. 513. 1760.
Elaphrium Jacq., Enum. Syst. Pl. Carib. 3. 1760.

Trees or shrubs; bark smooth or rough, the older bark peeling off in thin papery sheets or thick plate-like scales. *Leaves* odd-pinnate, bipinnate, or 1- to many-foliolate, usually crowded at the ends of the branches, completely deciduous during the dry season; leaflets opposite, membranaceous to coriaceous, petiolulate to sessile, the margins entire to toothed. *Inflorescences* axillary raceme-like panicles, appearing just before or simultaneously with to rarely after the new leaves; plants dioecious or polygamodioecious. *Flowers* small, 3–5-merous, usually functionally unisexual; sepals 3–5, connate at least basally, imbricate; petals 3–5, whitish to yellow, longer than the sepals, spreading and recurved, induplicate-valvate; stamens 6–10, the filaments subulate, free, inserted at the base of the disc, the anthers oblong, dorsifixed, smaller and abortive in carpellate flowers; disc annular, 6–10-lobed; gynoecium 2–3-carpelled, the ovary 2–3-lobed and -loculed, ovoid, sessile, small and abortive in staminate flowers, the ovules collateral, pendulous, 2 per locule, the style short, the stigma capitate, 2–3-lobed. *Fruits* drupaceous, subglobular to ellipsoid or obovoid, 2–3-angled, resinous, the exocarp and mesocarp coriaceous, dehiscing at maturity by 2–3 valves; pyrenes usually 1, usually 1-seeded; endosperm absent, the embryo straight or curved, the cotyledons foliaceous, contortuplicate, phanerocotyler.

A tropical and subtropical New World genus of perhaps 100 species, two occuring in Panama. The entire genus is in need of a careful revision like that done for the species of southwestern Mexico by McVaugh and Rzedowski (Kew Bull. 18: 317–382. 1965).

a. Leaflet margins crenate, the rachis winged; flowers 4-merous; fruits dehiscing by 2 valves . . . . . 1. *B. tomentosa*
aa. Leaflet margins entire, the rachis not winged; flowers 3- or 5-merous; fruits dehiscing by 3 valves . . . . . 2. *B. simaruba*

1. **Bursera tomentosa** (Jacq.) Tr. & Planch., Ann. Sci. Nat. Bot. Sér. 5. 14: 304. 1872. — FIG. 1.

Elaphrium tomentosum Jacq., Enum. Syst. Pl. Carib. 19. 1760.
Terebinthus tomentosa (Jacq.) W. F. Wight *in* Rose, Contr. U. S. Natl. Herb. 10: 122. 1906.
Bursera panamensis Pittier, Jour. Washington Acad. Sci. 11: 229. 1921.

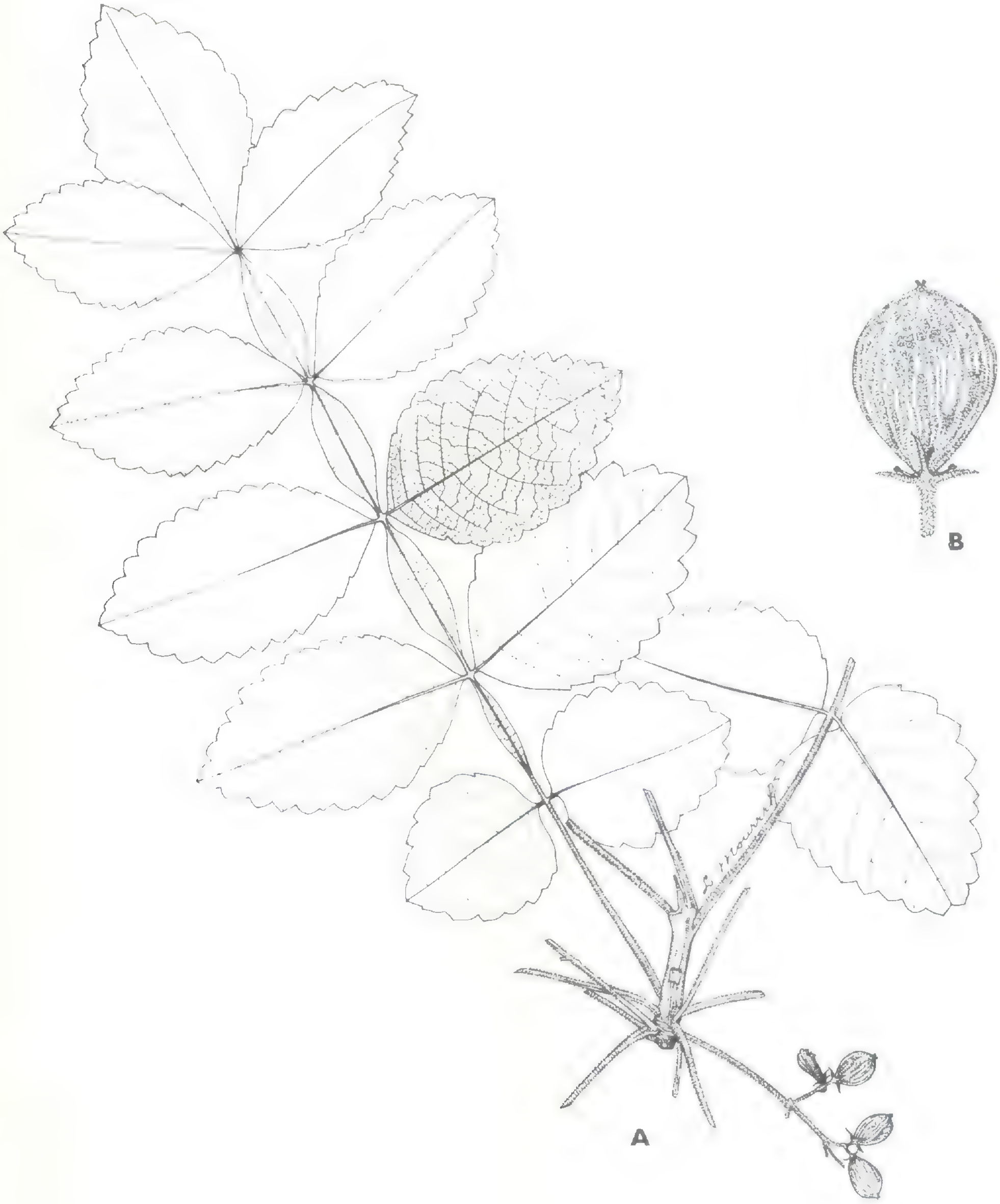

FIGURE 1. *Bursera tomentosa* (Jacq.) *Tr. & Planch.*—*A.* Habit (× 7/10).—B. Fruit (× 2½). [After *Dwyer 1114* (MO).]

Small *trees,* 5–10 m high; bark on the branches red, glabrate; branchlets tomentose, yellowish. *Leaves* odd-pinnate, grayish- or yellowish-tomentose, becoming less so with age, 5–20 cm long; petioles not winged, 10–44 mm long; leaflets (5–)7–11, elliptic to ovate elliptic or lanceolate-elliptic, slightly inequilateral, the laterals rounded to acute apically and obtuse basally, the terminals acute apically and basally, coriaceous, the margins crenate, tomentose and lighter beneath, less pubescent above with shorter trichomes, 27–62 mm long and 14–25 mm wide, the middle pairs usually largest, sessile or with petiolules to 1 mm long; rachis winged, the wing elliptic to oblanceolate, to 9 mm wide. *Inflorescences* tomentose, the staminate 1 cm long, the carpellate 2–6.5 cm long in fruit. *Flowers* 4-merous, with tomentose pedicels 3–6 mm long; staminate flowers with the sepals 4, connate basally, ovate, tomentose, ca. 1 mm long, the petals 4, ovate, pubescent, 1.5 mm long and less than 1 mm wide, thickened slightly and incurved apically, the stamens 8, the filaments less than 1 mm long, those opposite the sepals longer, the disc 8-lobed; carpellate flowers with the sepals 4, acute, 2–3 mm long, persistent in fruit, the stamens often persistent in fruit, the stigma 2-lobed, persistent in fruit. *Fruits* obovoid, glabrous, green, maturing copper-red and drying brown, 7–8 mm long and 5–7 mm in diameter, dehiscing by 2 valves; pyrenes 1, 1-seeded, bony, whitish, ovoid, convex, 6–8.5 mm long and 5–8 mm wide; seed coat black.

Following his description of *Bursera panamensis,* Pittier acknowledged its close relationship to *B. tomentosa.* The holotype specimen of the former falls well within the range of variation exhibited by the later in Panama.

This species occurs in Costa Rica, Panama, Columbia, Venezuela, and the Caribbean islands of Aruba, Bonaire, and Curaçao. In Panama known to flower in May, and to fruit in June through October, and December.

COCLE: Aguadulce, along outskirts of tidal belt, *Pittier 4493* (US, holotype of *Bursera panamensis*). HERRERA: Ocú, edge of 60 year-old forest, *Ebinger 1064* (MO, US). LOS SANTOS: Las Tablas, *Dwyer 1114* (MO). Pocrí, near Las Tablas, *Dwyer 114* (MO). PANAMA: Vicinity of Bejuco, *Allen 1806* (MO); typical dry deciduous scrub, common, *Allen 4515* (MO). Along road from Interamerican Highway to Coronado Beach, thorn forests and secondary thickets, *Duke 11810* (MO). Vicinity of Las Lajas Bridge, Panama National Highway, *Bartlett & Lasser 16644* (MO). Nueva Gorgona, near beach, *Duke 4503* (MO). VERAGUAS: Vicinity of Río Santa María ca. 5 mi. N of Santiago, *Blum & Tyson 617* (MO).

Bursera tomentosa occurs in the deciduous seasonal forests of Pacific Panama, the driest area on the isthmus. "Sometimes used for living fence posts" (fide *Allen 4515*). According to the label on *Blum & Tyson 617,* the fruit has a "lemon-like odor."

2. **Bursera simaruba** (L.) Sarg., Gard. & Forest 3: 260. 1890.

Pistacia simaruba L., Sp. Pl. 1026. 1753.
Bursera gummifera L., Sp. Pl. ed. 2. 471. 1762.
Terebinthus simaruba (L.) W. F. Wight *in* Rose, Contr. U. S. Natl. Herb. 10: 122. 1906.
Elaphrium simaruba (L.) Rose, N. Amer. Fl. 25: 246. 1911.

Trees, 5–20 m high; bark coppery-red, shiny, thin, peeling off in thin papery sheets to expose a smooth bright-green layer; branchlets glabrous to rarely yellow-

ish-woolly, becoming reddish-brown, covered with yellowish lenticels and conspicuously marked by large elevated cordate leaf scars. *Leaves* odd-pinnate, 21–35 cm long and 12–23.5 cm wide; petioles puberulent basally and sparingly pubescent above, or glabrous to rarely yellowish-woolly, 7–11.5 cm long; leaflets 5–7(–9), long-acuminate, inequilateral basally, the laterals broadly ovate to ovate-oblong, the terminals obovate, membranaceous to coriaceous, the margins entire, conspicuously lanate when young to nearly glabrate in age, becoming sparingly pubescent above, at least the veins pubescent beneath, slightly shiny above, paler beneath, the blades 4.5–14.5 cm long and 2.5–8 cm wide; petiolules pubescent to glabrous, 5–31 mm long; rachis not winged. *Inflorescences* usually glabrous, reddish; staminate 17–28 cm long, longer than the young leaves; carpellate 4–10.5 cm long, ca. as long as the young leaves. *Flowers* 3- or 5-merous, with glabrous pedicels 2–4 mm long in flower and 5–16 mm long in fruit; staminate 5-merous, the calyx shallowly 5-lobed, the lobes less than 1 mm long, the petals 5, ovate-elliptic, acute and incurved apically, 2–2.5 mm long and 1 mm wide, the stamens 10, ca. as long as the petals, the filaments 1.5 mm long, the disc 5-lobed; carpellate 3-merous, the calyx lobes 3, the petals 3, ovate, acute and incurved apically, 2 mm long and ca. 1 mm wide, the stamens 6, ca. half as long as the petals, the ovary 3-loculed, ovoid, ca. 2 mm high, the stigma 3-lobed. *Fruits* subglobular, pointed at both ends, slightly 3-angled, green to bright pink, maturing reddish-brown and drying brownish, 8–13 mm long and 7–9 mm in diameter, dehiscing by 3 obovate valves; pyrenes 1(–2), 1-seeded, 3-angled, bony, lenticular-ovoid, pinkish to whitish, attached to the pedicel by a persistent whitish column ca. 2 mm long.

Widespread throughout the Caribbean region, occurring from coastal northeastern Mexico through Central America, and southern Florida through the West Indies, to Panama, Colombia, and Venezuela. In Panama flowering from mid-March to mid-June, and collected in fruit in all months but September.

Bursera simaruba is both widespread and variable. Panamanian collections tend to have leaves and leaflets that are larger than those seen from elsewhere, and there is some variation within the isthmus in terms of leaflet size, shape, and pubescence. However, the combination of a thin, papery, coppery-red, peeling bark, and the complete loss of leaves during the dry season, make this tree immediately recognizable in the field. Perhaps there is more than one taxon represented by what has been called *B. simaruba,* as pointed out by Williams and Cuatrecasas (Trop. Woods 110: 32. 1959), but this cannot be determined until a thorough review is made of the genus.

CANAL ZONE: Barro Colorado Island, shore N of Fuertes House, *Woodworth & Vestal 741* (A); Fuertes Inlet, *Shattuck 1023* (F, MO); shoreline of Miller Peninsula S of Orchid Isle, *Croat 6723* (MO); Peña Blanca Point, *Shattuck 498* (F, MO), shoreline, large cove, *Croat* 8372 (MO); S of island (Barro Colorado Island?), *P. White 114* (F, MO). Farfan Beach area, *Tyson 1804* (MO). Fort Amador, on causeway and islands, *Tyson* 2023 (MO). Near beach at Fort Kobbe, *Duke 4219* (MO). Seedlings, across street from Gorgas Hospital, *Duke & Bristan 8302* (MO). Madden Dam, second growth, *Ebinger* 833 (MO); cut-over area across highway from Small Boat Landing, *Lewis et al. 5297* (MO). Vicinity of Miraflores Lake, moist shaded habitat, *G. White 159* (GH, MO). Sosa Hill, Balboa, brushy slope, occasional, *Standley 26483* (A, US). CHIRIQUI: Progreso, *Cooper & Slater 313* (US). Río San Cristóbal, 2 mi. W of David, alt. 150 ft, *Tyson 920* (MO). COCLE: Penonomé

and vicinity, alt. 50 1000 ft, *Williams 439* (US). DARIEN: Forests around Pinogana, *Pittier 6566* (US). Headwaters of Río Chico, heavy forest, alt. 500–700 ft, *Allen 4644* (MO). Río Puero, below village of Puero, *Duke 13117* (MO). HERRERA: Vicinity of Ocú, alt. 100 m, *Allen 4064* (MO). PANAMA: Cermeño, *Duyer & Robyns 111* (MO). Farfan Beach Road, *Kirkbride & Elias 67* (MO). Isla Espiritu Santo, common, *Duke 10432* (MO). Isla San José, East Harbor, rocky bluffs, *Erlanson 158* (GH, US); Main Beach, rocky coastal bluff, *Erlanson 107* (GH, US); rocky cliffs near sea, *Johnston 63* (GH). Isla Taboga, moist thicket, *Standley 27077* (US); moist wooded slope, common, *Standley 27928* (US); alt. ca. 0–186 m, *Woodson et al. 1503* (A, F, MO). 2 mi N of La Chorrera, secondary forest, *Lewis et al. 5190* (MO). Near Playa Río Mar, thorn forest, coastal scrub, and *Curatella* savanna, alt. 10–100 ft, *Duke 11781* (US). Río Mar, *Tyson et al. 2306* (US). Roadside savanna between Río Pacora and Chepo, *Duyer et al. 5114* (MO). Near Río Tapía, Juan Díaz region, *Maxon & Harvey 6638* (US). Near big swamp E of Río Tocúman, wet forest, *Standley 26583* (US). Sabana de Juan Corso, near Chepo, alt. 60–80 m, *Pittier 4670* (GH, US). VERAGUAS: Vicinity of Santa Fé-Río Santa María, alt. 1000 ft, *Allen 4423* (MO).

In Panama *Bursera simaruba* occurs in areas where the vegetation is deciduous seasonal forest, monsoon forest, and evergreen seasonal forest. It appears to be a species of advanced secondary growth.

Seemann (The Botany of the Voyage of *H. M. S. Herald,* p. 118) reported that, "This tree is of middle size; it is used for making fences; the wood is easy to cut, and the sticks, when put into the ground, soon produce young shoots. The gum that exudes from the stem is applied to wounds, and considered to have very beneficial effects." Comments on the labels of many recent collections attest that *Bursera simaruba* still has its uses, both medicinally and as living fence posts.

As is to be expected with a plant both common and economically important, a number of common names have been recorded for *Bursera simaruba.* Those used in Panama are *almácigo* (fide *Cooper & Slater 313* and *Standley 27928*), *carate* (fide *Standley 27928*), *gumbo-limbo* (fide *Woodworth & Vestal 741*), *hue-chi-chi* (fide *Allen 4644*), and *palo mulatto* (fide *Maxon & Harvey 6638*).

2. PROTIUM

Protium Burm. f., Fl. Ind. 88. 1768, *nom. cons.*

Tingulong Rumph., Auct. 54. 1755.
Icica Aubl., Hist. Pl. Gui. Fr. 1: 337. 1775.
Icicopsis Engl. *in* Mart., Fl. Bras. 12(2): 107. 1891.

Trees or shrubs. Leaves alternate, odd-pinnate or rarely 1-foliolate, petiolate; leaflets (1–)3–9(–13), usually distinctly acuminate, the margin usually entire, petiolulate; stipules absent. *Inflorescenses* axillary or rarely subterminal panicles or racemes. *Flowers* 4–5-merous, sessile or pedicellate, functionally unisexual; calyx 4–5-lobed, imbricate, persistent in fruit; petals 4–5, free, usually somewhat fleshy, induplicate-valvate, deciduous; stamens 8–10, slightly reduced and abortive in carpellate flowers, the filaments subulate to setose, free, inserted at the base of the disc, the anthers more or less oblong, dorsifixed to basifixed; disc 8–10-lobed, annular or cupuliform, thick, fleshy, pubescent to glabrous; gynoecium, 4–5-carpelled, the ovary 4–5-lobed and -loculed, ovoid or globose, pubescent to glabrous, abortive in staminate flowers, the ovules 2 per locule, subapical, collateral, pendulous, the style short, the stigma capitate, 4–5-lobed, usually persistent in fruit. Fruit drupaceous, globose to ovoid, ellipsoid, or turbinate, often

somewhat oblique, mesocarp fleshy and resinous, usually dehiscent by 2–5 valves; pyrenes 1–5, smooth, bony, 1-seeded; embryo straight, the cotyledons simple and plano-convex.

A tropical genus of perhaps 100 species, mainly American, but also with species in Madagascar, the Mascarenes, and Asia from India through the Malayan Archipelago. Seven taxa occur in Panama. Most species are South American, but in Panama only the two subspecies of *Protium tenuifolium* (Engl.) Engl. have South American affinities, the other five being Central American.

Protium is a taxonomically difficult genus. Many species have been based on scanty material, and a modern revision is badly needed. Sterile collections are almost impossible to identify to species without fertile material for comparison.

a. Leaves and inflorescences glabrous ..... 1. *P. panamense*
aa. Leaves (at least petioles, rachises, and petiolules) and inflorescences variously pubescent.
  b. Flowers 4-merous, distinctly pedicellate; fruits pedicellate, stipitate.
    c. Pedicels, calices, and petals yellowish-woolly ..... 2. *P. pittieri*
    cc. Pedicels, calices, and petals appressed-pubescent to sparsely puberulent.
      d. Petioles, rachises, and petiolules densely brownish-hirtellous ..... 3. *P. costaricense*
      dd. Petioles, rachises, and petiolules minutely puberulent.
        e. Leaflets broadly elliptic to oblong or ovate, abruptly acuminate, acute basally ..... 4. *P. glabrum*
        ee. Leaflets narrowly elliptic, obtuse or obtusely subacuminate, obtuse basally ..... 5. *P. inconforme*
  bb. Flowers 5-merous, subsessile or sessile; fruits sessile, not stipitate.
    f. Inflorescences and calices minutely puberulent ... 6. *P. tenuifolium* ssp. *mcleodii*
    ff. Inflorescences and calices ferrugineous-tomentose ..... 7. *P. tenuifolium* ssp. *sessiliflorum*

1. **Protium panamense** (Rose) I. M. Johnston, Contr. Gray Herb. 70: 72. 1924. — Fig. 2.

Icica panamensis Rose, N. Amer. Fl. 25: 260. 1911.

Trees or shrubs, 3–40 m high; branchlets striate, gray-barked, dotted with pale-brown lenticels, youngest parts minutely appressed-puberulent, soon glabrate. *Leaves* odd-pinnate, glabrous, the petioles, rachis, and petiolules often glaucous, 23–60 cm long; petioles striate, canaliculate, swollen apically and basally, 6–12.5 cm long; leaflets 3–7(–9), ovate-lanceolate to oblong, elliptic, or ovate, usually abrupty acuminate, rounded basally, coriaceous, the margins entire and repandous, the laterals inequilateral, 10.5–36.5 cm long and 4–12.5 cm wide, the terminals usually largest, to 38 cm long and 15 cm wide; petiolules striate, the laterals 11–32 mm long, the terminals to 85 mm long. *Inflorescences* compact axillary (occasionally cauliferous?) panicles, or rarely small racemes, branched from the base, glabrous, the carpellate to 7.5 cm long (to 10 cm long in fruit), the staminate to 10.5 cm long. *Flowers* yellow 4(–5)-merous; pedicels absent to 3.5 mm long in staminate flowers, 1–2 mm long in carpellate flowers; calyx cupuliform, 1.5 mm high, glabrous, 4(–5)-lobed, the lobes obtuse, acute apically, spreading; petals 4(–5), triangular, acute, more or less spreading, inflexed-apiculate, the margins papillose, 3 mm long, 1–1.5 mm wide; stamens 8(–10), 2 mm long; disc 8(–10)-lobed; ovary conical, 4(–5)-lobed, glabrous,

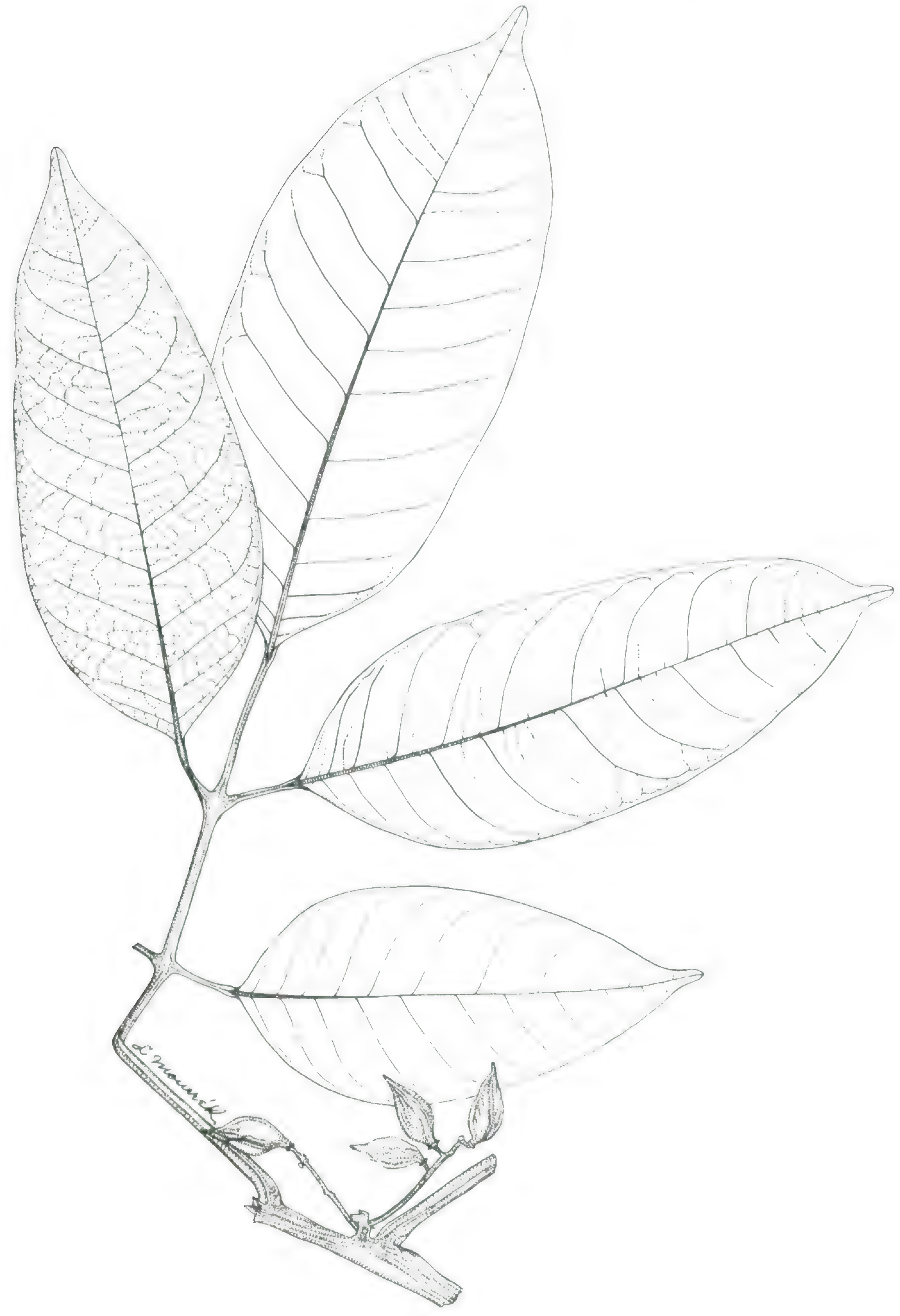

FIGURE 2. *Protium panamense* (Rose) I. M. Johnston, habit (× ½). [After *Tyson & Blum* 3755 (MO).]

ca. 1 mm high in staminate flowers, 2 mm high and tapering into the style in carpellate flowers, the stigma 4(–5)-lobed, persistent in fruit. *Fruits* ellipsoid to ovoid, more or less angled when dry, apiculate, stipitate, glabrous, green to yellow, becoming reddish at maturity, the mesocarp thick, white, 17–26 mm long and 9–21 mm in diameter, dehiscing by 2–4 valves, the valves red within; pyrenes 1(–4), white.

Endemic to Panama. Known to flower in January, February, April, July, August, September, and October, but collected in fruit in every month.

BOCAS DEL TORO: Almirante region, Cricamola, *Cooper 517* (F, US); Daytonia Farm, *Cooper 433* (F, GH, US). Vicinity of Chiriquí Lagoon, Darkland, *von Wedel 2625* (GH, MO, US); Fish Creek Hills, *von Wedel 2407* (GH, MO, US); Old Bank Island, *von Wedel 2106, 2115* (both GH, MO, US). Duwebdulup Peak, N of Río Terebe across from Quebrada Huron, alt. 300–900 ft, *Kirkbride & Duke 563* (MO). Vicinity of Río Toro Amarillo, Finca Vieja, alt. ca. 200 m, *Solis Rojas 434* (MO). CANAL ZONE: Agua Clara Reservoir, *Stevens 583* (US). Barro Colorado Island, *Bailey & Bailey 103, 319* (both F), *Brown 34, 38* (both F), *Dwyer 1435* (F, MO), *Kenoyer 677* (US), *Knight 12* (F), *Zetek 3467* (F); shores, *Bangham 405* (A, F, US), *424* (A, F); NE shore, *Salvoza 858* (A); NE to N shore, *Salvoza 884* (A); W side, *Wilson 125* (F, MO); shoreline N of dock, *Croat 7124* (MO); shoreline S of Colorado Point, *Croat 7866* (MO); shore of cove N of Drayton House, *Woodworth & Vestal 559* (A, F, MO); Fairchild Point, *Croat 4832* (MO); bohio at shore of cove S of French Lock Site, *Woodworth & Vestal 462* (A, F, MO); W side of Gross Point Peninsula, *Croat 5087* (MO); forest along shore E of Lab, *Killip 40015* (US); shore 2 mi. E of Lab, *Woodworth & Vestal 490* (A, F, MO); near #8 Light House Clearing, *Croat 6384* (MO); E edge of Orchid Island near French Cut and Gross Point, *Croat 8389* (MO); shoreline of large cove S of Orchid Island near Miller Trail, *Croat 6600* (MO); Salud Point, *Croat 4235* (MO); shore W of Salud Point, *Woodworth & Vestal 425* (A, F, MO); shoreline of E side of large cove E of Slothia Island, *Croat 6067* (MO); shoreline of large cove SW of Slothia Island, *Croat 7350* (MO); E shore of cove S of N tip of Slothia Island, E of dump cove, *Oppenheimer 66-8-11-1337* (MO); Snyder-Molino Trail, *Ebinger 9* (MO, US); Snyder-Molino Trail 1, *Shattuck 1172* (F, MO, US); Snyder-Molino Trail 250, *Croat 4409* (MO). Vicinity of Hill C-6, Camp Pina, Fort Sherman, *Duke 4397* (MO). Road from Fort San Lorenzo to Fort Sherman, *Tyson & Blum 3755* (MO). Frijoles, *Stevens 1269* (US). Gatun Railroad Station, *Hayes 1* (A, F, GH, US; probably isotypes of *Icica panamensis*), *Hayes 462* (US, holotype of *I. panamensis*). Forest along Pavon Road, *Johnston 1540* (A). Sheltered shaded seacliff, mouth of Tortuguilla Creek, *Johnston 1520* (A). COCLE: Boca del Toabré, confluence of Río Toabré & Río Coclé del Norte, advanced secondary forest, *Lewis et al. 5482* (MO). COLON: Camp Betija, Donoso District, alt. 60–150 m, *Holdridge 6256* (MO). Vicinity of Camp Pina, alt. 0–50 m, *Allen 3429* (MO). In forests, Loma de La Gloria, near Fató (Nombre de Dios), alt. 10–104 m, *Pittier 4082* (F, GH, US). SAN BLAS: Isla Pino near Mulatuppo, alt. to 200 ft, *Elias 1717* (MO).

Protium panamense is the most wide-spread species of the genus in Panama, although known only from the Caribbean side of the Continental Divide, and is to be expected in both Costa Rica and Colombia. It occurs in evergreen seasonal forests and monsoon forests. Like *P. glabrum*, it has been reported to have "stilt roots similar to those of *Cecropia*" (fide *Johnston 1540*). According to Dr. Thomas B. Croat (personal communication), "At maturity one valve usually falls exposing the fleshy-white mesocarp, often against the red interior of the other valve." No common names have been recorded by collectors.

2. **Protium pittieri** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica pittieri Rose, N. Amer. Fl. 25. 260. 1911.

Trees or shrubs, to 8 m high; branchlets striate, yellowish-woolly when young, becoming almost glabrate. *Leaves* odd-pinnate, 35–48 cm long; petioles striate,

canaliculate above, yellowish-woolly when young, becoming minutely puberulent, 7.5–17.5 cm long; leaflets 3–7, obovate, ovate, or lanceolate to elliptic, abruptly short-acuminate, the laterals inequilateral basally, subcoriaceous, the margins undulate, yellowish-woolly, becoming glabrate, the midribs becoming minutely puberulent above and beneath, the laterals 16–22 cm long and 7–9.5 cm wide, the terminals 16–23 cm long and 8–13 cm wide; petiolules canaliculate, thickened apically, yellowish-woolly when young, becoming minutely puberulent, the laterals 12–18 mm long, the terminals 38–62 mm long. *Inflorescences* axillary panicles, branched from the base, yellowish-woolly, becoming appressed-pubescent, 1–7 cm long in bud, to 9.5 cm long in fruit. *Flowers* yellow, 4-merous; pedicels yellowish-woolly, ca. 1 mm long; calyx yellowish-wooly, 4-lobed, the lobes triangular, acute; petals 4, yellowish-woolly. *Fruits* oblong, more or less acute apically, stipitate, sparsely appressed-pubescent, brown, with abundant yellowish lenticels, the mesocarp thick, white, 3–4 cm long and 1.5–3 cm in diameter, dehiscing by 2–4 valves; pyrenes 1–2, brownish.

Costa Rica and Panama. In Panama known to flower in November and to fruit in April.

BOCAS DEL TORO: Río Teribe, between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 462* (MO). Vicinity of Chiriquí Lagoon, Water Valley, *von Wedel 1566* (F, GH, MO).

Protium pittieri occurs in areas of evergreen seasonal forest. The fruits are edible (fide *Kirkbride & Duke 462*).

3. **Protium costaricense** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica costaricensis Rose, N. Amer. Fl. 25: 259. 1911.
Icica confusa Rose, op. cit. 25: 260. 1911.
Protium confusum (Rose) Pittier, Contr. U. S. Natl. Herb. 20: 479. 1922.
Protium salvozae Standley, Jour. Arnold Arbor, 11: 122. 1930.

Trees, 4–8 m high; branchlets densely brownish-hirtellous and minutely puberulent, marked with light lenticels. *Leaves* odd-pinnate, 13–44 cm long, 10.5–24 cm wide; petioles canaliculate, 2.5–6.5 cm long, they and rachises densely brownish-hirtellous and minutely puberulent; leaflets (3–)5–7(–9), elliptic, oblong, ovate, or obovate, slightly inequilateral, abruptly acuminate, cuneate basally, subcoriaceous, margins entire, brownish-hirtellous and minutely puberulent, especially on the veins, becoming glabrate between the veins, the laterals 6–14 cm long and 2.5–6 cm wide, the terminals 8.5–11.5 cm long and 3.5–5.5 cm wide, the lowermost pair smallest; petiolules slightly swollen apically, densely brownish-hirtellous and minutely puberulent, the laterals 5–10 mm long, the terminals 18–26 mm long. *Inflorescences* axillary panicles, few-branched from the base, densely brownish-hirtellous and minutely puberulent, becoming glabrate, 1–5 cm long. *Flowers* yellow, 4-merous; pedicels sparsely puberulent, 1.5–2 mm long, calyx cupuliform, 1 mm high, 4-lobed, the lobes broadly triangular, acuminate, a little shorter than the tube, sparsely puberulent; petals 4 oblong-triangular, the upper half spreading, sparsely puberulent on both surfaces, the margins papillose, inflexed apiculate apically, 3 mm long and 1.5 mm wide; stamens 8, 2 mm high in carpellate flowers, the filaments subulate, dilated

basally; disc 8-lobed, annular, glabrous, less than 1 mm high, surrounding the base of the ovary; ovary ovoid, pubescent, tapering into the style, 1.5 mm high in carpellate flowers, the style persistent in fruit, the stigma 4-lobed. *Fruits* obliquely ovoid, acute, stipitate, puberulent to almost glabrate, the exocarp red, spotted with lighter lenticels, 13–16 mm long and 11–12 mm in diameter; pyrenes 1, white.

Costa Rica and Panama. In Panama known to flower in February and to fruit in May and September.

CANAL ZONE: Barro Colorado Island, wet forest, *Standley 41081* (US); near Cabin 2, *Salvoza 948* (F); clearing at Drayton House, *Croat 5769, 8262* (both MO); shore of cove W of Drayton House, *Woodworth & Vestal 605* (A, F, MO); Drayton House to Armour Cabin, *Bangham 513* (F holotype of *P. salvozae;* A, US, isotypes); Wheeler Trail, 1600, *Croat 6295* (MO).

According to the label on *Croat 8262,* the plant has "no strong odor," and the bark is "like strong sandpaper." It occurs in monsoon forests.

4. **Protium glabrum** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica glabra Rose, N. Amer. Fl. 25: 259. 1911.
Protium ternatum Pittier, Contr. U. S. Natl. Herb. 20: 478. 1922.
Protium copal var. *glabrum* (Rose) Swart, Rec. Trav. Bot. Néerl. 39: 332. 1942.
Protium copal var. *ternatum* (Pittier) Swart, op. cit. 39: 333. 1942.

Trees, 6–12 m high. *Leaves* odd-pinnate, becoming more or less glabrate, to 30 cm long; petioles canaliculate, minutely puberulent, 2–8.5 cm long; leaflets 3–5(–9), broadly elliptic to oblong or ovate, slightly inequilateral, abruptly acuminate, acute basally, subcoriaceous, minutely puberulent, becoming glabrate, 6.5–19 cm long and 2–8 cm wide; petiolules canaliculate, thickened apically and basally, minutely puberulent, the laterals 8–13 mm long, the terminals 2–5 cm long. *Inflorescences* axillary panicles, slender, branched from the base, usually few-flowered, sparingly appressed-pubescent, 1–13.5 cm long. *Flowers* yellow, 4-merous; pedicels sparingly appressed-pubescent, 2–2.5 mm long; calyx shallowly 4-lobed, the lobes broad and rounded, spreading, sparingly appressed-pubescent, ca. 1 mm high; petals 4, broadly ovate, spreading apically, sparingly appressed-pubescent, pubescent adaxially, the margins papillose, 3 mm long and 1.5 mm wide; stamens 8, the filaments subulate, 1.5 mm long; disc 8-lobed, sulcate, thick, glabrous, covering ca. half the ovary in carpellate flowers and as high as the ovary in staminate flowers, forming a prominent glabrous collar at the base of the fruit; ovary ovoid, appressed-pubescent in carpellate flowers, glabrous in staminate flowers, the stigma 4-lobed. *Fruits* ovoid, apiculate, stipitate, minutely pubescent, especially apically and basally, reddish, the mesocarp pink or white, 11–25 m long and 10–17 mm in diameter; pyrenes (1–)2–3, green.

This inaptly-named species was described by Rose as having glabrous branches, leaflets, and ovaries. However, examination of the holotype specimen [*Tonduz 6682,* Costa Rica (US)] shows this not to be the case.

Costa Rica and Panama. In Panama known to flower in July and August, and to fruit in May, July, and August.

CANAL ZONE: 12 mi. S of Colón, *Tyson et al. 4475* (GH, MO, US). Vicinity of Río Providencia, in forest understory, *Blum & Tyson 2327* (MO). Hills SW of Gatún, in forest, alt. 600 ft, *Johnston 1586* (A, MO). COLON: Achiote, *Tyson et al. 4540* (MO). Along Río Fató above Nombre de Dios, in forests or thickets, alt. 10–100 m. *Pittier 3949* (US), *4190* (US, holotype of *P. ternatum;* GH, US, isotypes), *4191* (F, US). PANAMA: Cerro Jefe, forest edge and road bank, alt. ca. 2900 ft, *Dwyer & Gauger 7339* (MO).

Protium glabrum is found on the Caribbean side of the Continental Divide in areas of monsoon forest and seasonal evergreen forest. In fruits containing two pyrenes, invariably the opposite carpels are fertile, the two between them being sterile.

The label on *Johnston 1586* states that the plant had "*Cecropia*-like stilt-buttresses." Butressing is not uncommon in the Burseraceae, but few New World species have been reported to form them.

5. **Protium inconforme** Pittier, Contr. U. S. Natl. Herb. 20: 478. 1922.

Protium copal var. *inconforme* (Pittier) Swart, Rec. Trav. Bot. Néerl. 39: 333. 1942.

Trees, to 6 m high. *Leaves* odd-pinnate, 8–22 cm long; petioles canaliculate, minutely puberulent, 11–19 mm long; leaflets 3–7, some often missing, narrowly elliptic, slightly inequilateral, obtuse or obtusely subacuminate, obtuse basally, the midvein minutely puberulent above to glabrate, 6–14.5 cm long and 1.5–4 cm wide; petiolules canaliculate, somewhat swollen apically, minutely puberulent, the laterals 2–6 mm long, the terminals 8–24 mm long. *Inflorescences* axillary racemes, branched from the base, few-flowered, minutely puberulent, 6–20 mm long. *Flowers* 4-merous; pedicels appressed-puberulent; calyx appressed-puberulent, ca. 1 mm high, 4-lobed, the lobes broad, short, obtuse; petals 4, spreading apically, appressed-puberulent, pubescent adaxially, inflexed-apiculate, the margins papillose, 2–2.5 mm long and 1–1.5 mm wide; stamens ca. 1 mm high in carpellate flowers; disc glabrous, surrounding the ovary only basally; ovary ovoid, appressed-pubescent, ca. 1 mm high, the style persistent in fruit, the stigma 4-lobed. *Fruits* oblong or ellipsoid to ovoid, apiculate, stipulate, green flushed dull purple, pubescent when young, becoming glabrate except apically, 15–18 mm long and 6–13 mm in diameter; pyrenes 1–2.

Endemic to Panama. Known to flower in March and April, and to fruit in December, February, and March.

CHIRIQUI: Around Caldera, alt. 200–300 m, *Pittier 3350* (US, holotype; F, GH, isotypes). 12.4 mi. N of David, edge of steep river bank, *Lewis et al. 707* (MO). LOS SANTOS: Guanico, forest of espavé, caoba, and cedro espino, alt. 117 ft, *Stern et al. 1840* (MO, US). Ridge W of Río Pedregal, *Holdridge 6237* (MO).

The sterile specimen *Holdridge 6201* (MO) from "LOS SANTOS: Area east of Cambutal on lower hills" is probably this species, but it is impossible to tell from vegetative material alone.

This species is known from southwestern Panama in areas of monsoon forest or deciduous seasonal forest. It is called *chutra* (fide *Holdridge 6237*). This is also the name ascribed to it by Pittier, following his type description.

6. **Protium tenuifolium** ssp. **mcleodii** (I. M. Johnston) D. M. Porter, Ann. Missouri Bot. Gard. 56: 475. 1969[1970].

Protium mcleodii I. M. Johnston, Sargentia 8: 164. 1949.

Trees, 6–16 m high; branchlets somewhat glaucous, minutely puberulent, becoming glabrate. *Leaves* odd-pinnate, 17.5–38.5 cm long and 14.5–28 cm wide; petioles canaliculate, minutely puberulent, soon glabrate, 4–11 cm long; leaflets 7–11, oblong, abruptly acuminate, obtuse and inequilateral basally, membranaceous to subcoriaceous, often minutely papillose, the margins entire, 5–15 cm long and 2–5 cm wide, the lowermost pair smallest and reflexed; petiolules swollen apically and basally, minutely puberulent, soon glabrate, the laterals 4–11 mm long, the terminals to 24 mm long. *Inflorescences* axillary panicles, minutely puberulent; staminate with the branches widely spreading, 6.5–10 cm long and 3.5–7.5 cm wide; carpellate with the branches few, divaricate, 4.5–9.5 cm long. *Flowers* yellowish, 5-merous, subsessile to sessile; staminate with the calyx 5-lobed, less than 1 mm long, the petals 5, 1.5 mm long and ca. 0.5 mm wide, the stamens 10, 1 mm long, the disc 10-lobed, tomentulose; carpellate with the calyx cupuliform, minutely puberulent, 5-lobed, the lobes triangular, less than 1 mm long, subequal to the tube, the petals 5, thick, not reflexed, glabrous, slightly ridged abaxially, inflexed-apiculate, the margins papillose, 2.5 mm long and 1 mm wide, the stamens 10, the disc 10-lobed, tomentulose, the ovary ovoid, tomentulose, immersed in the disc basally, ca. 1 mm high, the stigma 5-lobed, usually persistent in fruit. *Fruits* obliquely ovoid to turbinate, minutely puberulent, becoming glabarate, 13–16 mm long and 8–19 mm in diameter; pyrenes 1(–5).

Endemic to Panama. Known to flower in March, April, May, and November, and to fruit in March, April, May, and July.

DARIEN: Forest near Piriaque, peak 800–1000 ft. alt., *Duke 8061* (MO). PANAMA: San José Island, in forest near thickets, area W of East Loop, *Johnston* 586 (GH); vicinity of Goat Farm, near Río Mata Puerco, *Erlanson 186* (GH, US); forest back of Naval Station, *Johnston 420* (GH, US), *562* (GH, MO); edge of thicket, Naval Station Road, *Johnston* 557 (GH, holotype; MO, US, isotypes); valley of Río Mata Puerco, *Erlanson 67* (GH); near South Beach, *Erlanson 45* (US); understory tree in *Tetragastris* forest, between South Road & Playa Grande, *Johnston* 654 (GH, US). Trapiche Island, *Miller 1880, 1891, 1904* (all US), *Allen 2632* (F, GH).

Protium tenuifolium is a widespread species of northern South America. The two Panamanian subspecies are the northernmost representatives of this taxonomically difficult group.

This subspecies occurs in monsoon forests. Unlike most Panamanian Burseraceae, both flowers and fruits often are found on the same inflorescence. Known as *Conejo* (fide *Miller 1880*).

7. **Protium tenuifolium** ssp. **sessiliflorum** (Rose) D. M. Porter, Ann. Missouri Bot. Gard. 56: 475. 1969[1970].—FIG. 3.

Icica sessiliflora Rose, N. Amer. Fl. 25: 259. 1911.
Protium sessiliflorum (Rose) Standley, Jour. Washington Acad. Sci. 15: 459. 1925.
Protium neglectum var. *panamense* Swart, Rec. Trav. Bot. Néerl. 39: 205. 1942.
Protium neglectum var. *sessiliflorum* (Rose) Swart, op. cit. 39: 385. 1942.

Trees, 5–18 m high; branchlets brown, glabrous, dotted with paler lenticels. *Leaves* odd-pinnate, 31–48 cm long; petioles canaliculate, sparsely puberulent, soon glabrate, 7.5–13 cm long; leaflets 5–9(–13), oblong to oblanceolate, obovate, or ovate, inequilateral, abruptly acuminate, acute to obtuse basally, coriaceous, glabrous, usually minutely papillose, the margins undulate, 10–27 cm long and 5–12 cm wide, the basal pair usually reflexed; petiolules thickened apically and sometimes basally, sparsely puberulent, the laterals 6–30 mm long, the terminals 20–67 mm long. *Inflorescences* axillary panicles, the branches spreading, ferrugineous-tomentulose; staminate 11–24.5 cm long and to 16 cm in diameter; carpellate stout, branched from the base, 6–16 cm long and to 6.5 cm in diameter. *Flowers* 5-merous, sessile; staminate with the calyx 5-lobed, 1 mm high, ferrugineous-pubescent, the petals 5, lanceolate, glabrous, somewhat keeled abaxially, inflexed-apiculate, the margins papillose, 2.5–3 mm long and ca. 1 mm wide, the stamens 10, the filaments subulate, 1 mm long, the disc 5-lobed, ferrugineous-tomentose; carpellate with the disc ferrugineous-tomentose, the ovary 5-lobed, the stigma 5 lobed, persistent on the fruit. *Fruits* ovoid, somewhat oblique, fleshy, 2–5-lobed, sessile, green, maturing red, tomentulose when young, becoming glabrate except apically, dotted with minute ferrugineous papillae, the mesocarp white, 12–16 mm high and 8–20 mm in diameter, dehiscing by 2–5 valves; pyrenes 1(–5).

Costa Rica and Panama. In Panama known to flower from January through May and in September, and to fruit in February and May through September.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 294* (F, holotype of *P. neglectum* var. *panamense*), *Duver 1470*, *Tyson 4204* (both MO); wet forest, *Standley 40984* (US); NE to N shore, *Salvoza 888* (A); W side on shore, *Wilson 134* (MO); large cove N of dock, *Croat 6099* (MO); along shore E of dock, *Ebinger 217* (MO, US); shoreline S of Colorado Point, *Croat 8754* (MO); shoreline between small cove N of dock and Fairchild Point, *Croat 6233* (MO); Gatun Lake to point where one turns from Canal, *Bangham 427* (A, F); frequent near Laboratory, etc., *Kenoyer 422* (US); shoreline from tip of Pearson Trail peninsula SW to third large cove, *Croat 5404* (MO); shoreline, Peña Blanca Bay, *Croat 8309* (MO); second cove E of Slothia Island, *Croat 5151* (MO); Wheeler Trail, *Starry 125* (MO), *139* (F). Roadside woods, George Green Memorial, Madden Forest, *Duver & Elias 7523* (MO). Road K 9, along Río Cocolí, *Stern et al. 10* (GH, MO, US). CHIRIQUI: Progreso, *Cooper & Slater 259*, frequent in upper part of understory, *169* (both F, US). DARIEN: Piriaque, camp at river, *Tyson et al. 4743* (MO); forest 1–4 mi. N of Puero, *Duke 13022* (MO); Río Tuqueza below Quebrada Venado, *Bristan 1082* (MO); cuipo forests near Santa Fé, *Duke 12895* (MO). PANAMA: Rocky slopes along Río Chagres above Alhajuela, alt. 30 100 m, *Pittier 3522* (US). Woods along Panamerican Highway ca. halfway between El Llano and Río Mamoní, *Duke 5628* (MO.).

This wide-ranging subspecies occurs in areas of monsoon forest and seasonal evergreen forest. Common names reported are *anime* (fide *Standley 40984*), *chutras* (fide *Cooper & Slater 169*), and *comida del mono* (fide *Cooper & Slater 259*).

3. TETRAGASTRIS

Tetragastris Gaertn., Fruct. Sem. Pl. 2: 130. 1790.

Hedwigia Swartz, Prodr. Veg. Ind. Occ. 4. 1788, non *Hedwigia* Beauv., Mag. Encycl. 5: 304. 1804, *nom. cons.*

Trees or shrubs. *Leaves* alternate, odd-pinnate, membranaceous to coriaceous; leaflets 5–11, acuminate apically, the laterals inequilateral basally, the margins

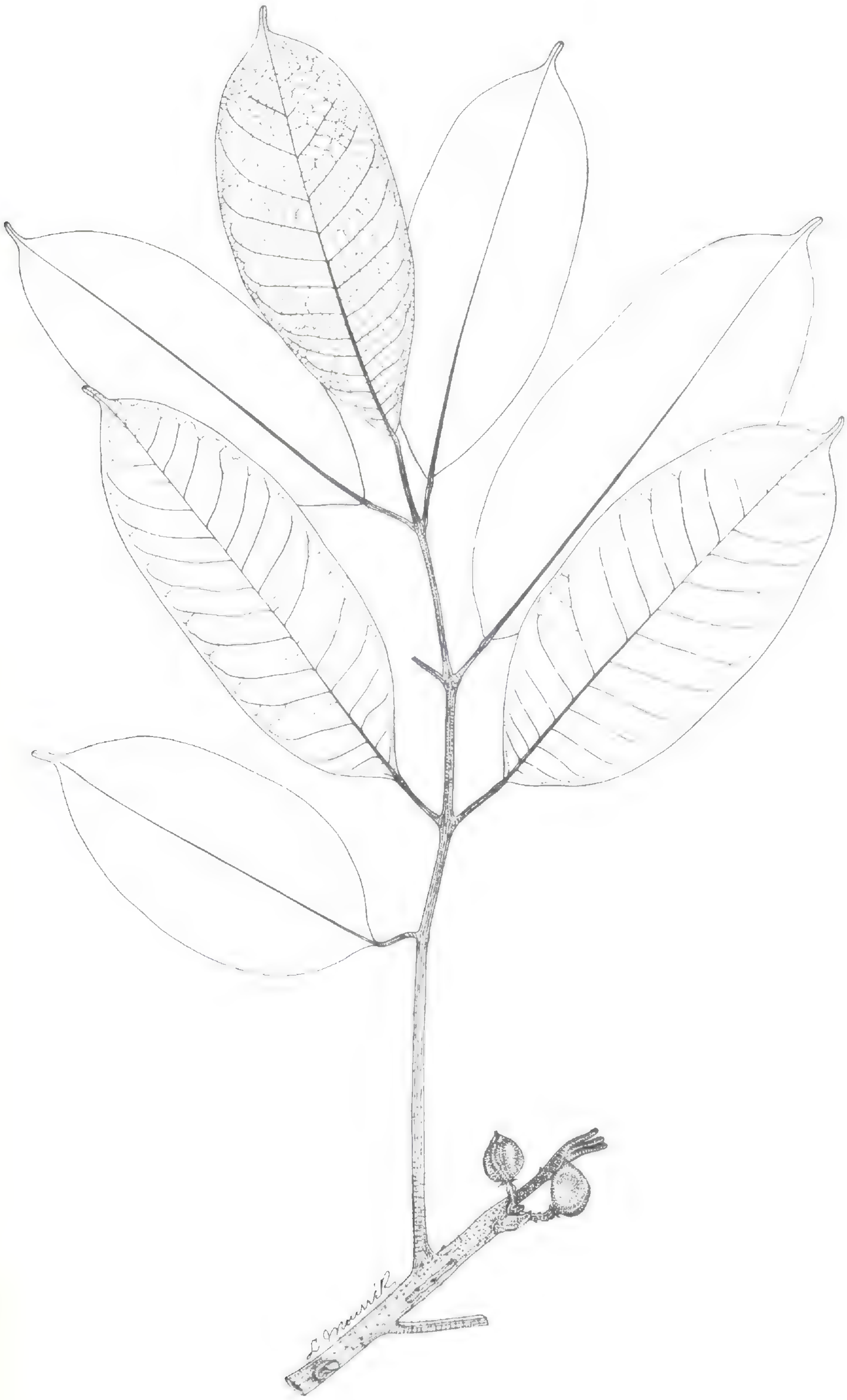

FIGURE 3. *Protium tenuifolium* ssp. *sessiliflorum* (Rose) D. M. Porter, habit (× 3/8). [After *Tyson 4204* (MO).]

entire. *Inflorescences* axillary to subterminal or terminal panicles, shorter than the leaves; plants dioecious or polygamous. *Flowers* small, 4–5-merous, calyx synsepalous, cupular, 4–5-lobed, lobes short, equal, imbricate, and persistent in fruit; corolla sympetalous, tubular, fleshy, 4–5-lobed, lobes alternating with the calyx-lobes, equal, induplicate-valvate, inflexed-apiculate; stamens 8–10, the filaments free or rarely adnate to the petals, inserted at the base of the disc, the anthers introrse, dehiscing longitudinally; disc thick, fleshy, glabrous, 8–10-lobed; gynoecium 4–5-carpelled, the ovary 4–5-lobed and -loculed, partly immersed in the disc, the ovules apical, pendulous, 2 per locule, the style short, the stigma 4–5-lobed. *Fruits* drupaceous, valvate, 2–5-lobed, 1–5-loculed, the exocarp coriaceous, the mesocarp thick and resinous, septicidally dehiscent; pyrene 1–5, smooth, woody, 1-seeded, separated by a distinct layer of mesocarp; endosperm absent, the cotyledons simple, plano-convex.

A Neotropical genus of about a dozen species occuring from Brazil northward through the West Indies to Hispaniola and through Central America to British Honduras. Two species are known from Panama.

a. Flowers 5-merous; leaves sparingly pubescent ..... 1. *T. panamensis*
aa. Flowers 4-merous; petioles and the midveins of the leaflets densely yellowish-tomentose ..... 2. *T. tomentosa*

1. **Tetragastris panamensis** (Engl.) O. Kuntze, Rev. Gen. Pl. 1: 107. 1891. —FIG. 4A–C.

Hedwigia panamensis Engl., Bot. Jahrb. Syst. 1: 42. 1881.
Tetragastris stevensonii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 216. 1929.
Tetragastris panamensis var. *hirtella* Swart, Rec. Trav. Bot. Néerl. 39: 207. 1942.

Trees or rarely shrubs, 3–35 m high; crown widely-spreading; branches grayish, the branchlets densely yellowish-puberulent when young, becoming glabrate and reddish and dotted with elliptical reddish lenticels when older. *Leaves* 15–37 cm long; petioles striate, with scattered minute trichomes, canaliculate above, broadened basally, 4–14 cm long; leaflets 7–9(–11), coriaceous, sparingly pubescent, 5–21 cm long and 17–72 mm wide, the terminals oblong to oblanceolate or elliptic, broadly obtuse to long-acuminate apically, usually larger, the laterals oblong-lanceolate, long-acuminate, inequilateral basally, the lowermost pair smallest and often reflexed; petiolules sparingly pubescent, canaliculate above, swollen apically and/or basally, the laterals 2–12 mm long, the terminals 12–45 mm long. *Inflorescences* axillary, loosely-branched, slender to spreading, yellowish-puberulent, 3–15 cm long; buds yellow, sometimes tinged with red. *Flowers* whitish to greenish-yellow or yellow, 5-merous; pedicels yellowish-puberulent, ca. 1 mm long; calyx broadly cupular, shallowly lobed, yellowish-puberulent, 2–2.5 mm wide and 1–1.5 mm high, the lobes 5, broadly rounded, spreading a little; corolla yellowish, densely yellowish-puberulent without, glabrous within, 3–5 mm long, the lobes 5, thick, acute, 1–2 mm long; stamens 10, 1 mm long, ca. ½ as long as the corolla tube, covering the ovary in carpellate flowers, the filaments short, inserted at the base of the disc between the lobes, the anthers sagittate, 3–5 times as long as the filaments, smaller and abortive in carpellate flowers; disc annular, 10-lobed, as high as the filaments; ovary

ovoid, 5-lobed, 5-loculed, 1.5 mm in diameter, sparingly pubescent, and reaching to above the stamens in carpellate flowers, pyramidal, glabrous, and abortive in staminate flowers, surrounded basally by the disc, the style pyramidal, ca. 1

FIGURE 4. *Tetragastris*.—A–C. *T. panamensis* (Engl.) O. Kuntze.—*A*. Habit (× ⅔). —B. Flower (× 6½).—C. Fruit (×2⅓). [A, after *Stern et al. 520* (MO); B, after *Dwyer 1669* (MO); C, after *Holdridge 6250* (MO).]—D. *T. tomentosa* D. M. Porter, flower (× 6½). [D, after *von Wedel 2398* (MO).]

mm high, persistent on the fruit, the stigma 5-lobed, spherical. *Fruits* fleshy when immature, becoming broadly more or less turbinate capsules, 2–5-lobed, 1–5-loculed, 1.5–2.5 cm high and 1.5–3 cm in diameter, broadest above the base and sloping toward the obtuse apex, attached to the pedicel at the middle of the centrally depressed broader end, usually slightly ridged between the lobes, dehiscent by 2–5-valves, the interior surfaces of the valves red, the exocarp green, becoming purplish, red, or brown, mesocarp reddish, white at dehiscence, firm, gelatinous, 1–2 mm thick, sparingly hirtellous to usually glabrate; pyrenes 1–5, smooth, white, 12–13 mm high.

Tetragastris panamensis var. *hirtella* was erected by Swart on the basis of the presence of hirtellous ovaries and fruits. However, the examination of a large series of specimens of *T. panamensis*, from both Central and South America, shows that this trait does not warrant taxonomic recognition. All ovaries examined were pubescent in carpellate flowers and glabrous in staminate flowers, while fruits ranged from sparingly hirtellous to usually glabrate.

This species occurs in British Honduras, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, the Guianas, Brazil, and Peru. In Panama it is known to flower in June, July, August, October, and December, and to bear fruit in all months but December.

CANAL ZONE: Barro Colorado Island, *Kenoyer 426A* (US), *Shattuck 631* (MO); Fuertes Cove, *Croat 8122* (MO); shoreline of large cove leading to Fuertes House, *Croat 6823, 6839* (both MO); E shore of cove S of N tip of Slothia Island, *Oppenheimer 66-3-28-1358* (MO); Snyder-Molino Trail 325, *Croat 6739, 8081* (both MO), 50 m N of trail, *Croat 8101* (MO). Coco Solo, dense woods with man-made drainage ditches, *Duyer & Duke 7874* (MO). Near beach at Fort Kobbe, wooded S slope facing ocean, *Duke 4729* (MO). COCLE: Penonomé and vicinity, alt. 50–1000 ft, *Williams 201* (US). COLON: Donoso district, Camp Betija, alt. 60 150 m, *Holdridge 6250* (MO). DARIEN: Vicinity of Cana, alt. 2500 ft, *Stern et al. 520* (GH, MO, US). Piriaque, camp at river, *Tyson et al. 4747* (MO); forest near Piriaque, peak 800 1000 ft high, *Duke 8060* (MO); Pico Piriaque, *Duke 8150* (MO). Vicinity of Piñas, *Duke 10596* (MO). Forest 1 4 mi. N of Puero, *Duke 13042* (MO). Puerto Santa Dorothea, *Duyer 2214* (MO, US). Punta Guayabo Chiquita, steep hills near shore, *Stern & Chambers 164* (A, F, MO, US). Río Pucro, below Pucro, *Duke 13121* (MO). PANAMA: E slope of Cerro Jefe, in *Clusia* forest, alt. 2700 ft, *Tyson 3388* (GH, MO). El Cermeño, *Zetek 4997* (F, MO). Isla Espiritu Santo, *Duke 10447* (MO). Juan Díaz, moist thicket, *Standley 30647* (US). Vicinity of Pacora, alt. 0–20 m, *Allen 3451* (GH, MO, US). Gallery forest along Río Terable, near Panamerican Highway and El Llano, *Duke 5662* (MO). San José Island, *Johnston 658* (GH); thickets bordering Bald Hill, *Erlanson 300* (GH, US); Loop at Little Butch, *Johnston 911* (GH); Loop Road, dominant forest tree in Marino Basin, *Johnston 202* (GH); along stream in M-area, *Johnston 4* (GH, US); road SW of Red Hill, *Johnston 138* (GH, MO, US); Río Marino below Red Hill, along stream, *Johnston 555* (GH, US); valley of Rio Marino, Area 7a, *Erlanson 342* (GH, US); N fork of Río Marino, moist dense forest along stream, *Johnston 398* (GH); between South Road and Playa Grande, forming forest, *Johnston 275* (GH, MO). SAN BLAS: Without locality, *Cooper 290* (GH). Chucunaque, 2 10 mi. above Cuna-Darién boundary, *Duke 8571* (MO). Permí, *Cooper 265* (F, US). VERAGUAS: Canazas, bank of Río Canazas, *Tyson 3633* (MO). Isla de Coiba, *Dwyer 1633* (F, GH), *1669, 2320A* (both MO), *2327* (GH). Vicinity of Río Santa Maria, ca. 5 mi. N of Santiago, *Blum 625* (MO). WITHOUT LOCALITY: *Duchassaing*, 1851 (GH).

According to Johnston (Sargentia 8: 165. 1949), *Tetragastris panamensis* is an important forest tree on San José Island, where it may make up more than half of the canopy layer in both small or large tracts of forest. It is widespread in Panama, having been collected mainly on the Pacific side of the Continental

Divide. It occurs in areas of evergreen seasonal forest, monsoon forest, and deciduous seasonal forest.

The fruits of this species usually are described as indehiscent. The fruits are fleshy when immature, but they dehisce by from two to five valves when mature. Johnston (Sargentia 8: 166. 1949) gives a detailed description of the fruits of *Tetragastris panamensis*.

Common names reported for *Tetragastris panamensis* in Panama are *animé* (fide *Stern & Chambers 164*), *cedro macho* (fide *Duke 10596*), *fruta de loro* (fide *Duke 8060*) and *secuadro* (fide *Duke 8150*). A number of collectors have remarked on the aromatic sap of this species, and the label on *Johnston 275* states, "Fruit and herbage with a pleasant rather spicy terpentine odor." According to the label on *Duke 10596*, the fruits (probably the mesocarp only) are edible.

2. **Tetragastris tomentosa** D. M. Porter, Madroño 20: [in press]. — FIG. 4D.

A *tree* ca. 8 m high; branchlets densely yellowish-tomentose. *Leaves* 37 cm long or longer and to 24.5 cm wide; petioles striate, densely yellowish-tomentose, canaliculate above, 84 mm long; leaflets 7(?), membranaceous, elliptic to ovate, abruptly acuminate, slightly inequilateral basally, the main vein densely yellowish-tomentose below, minutely puberulent above, the secondary veins and blade with scattered trichomes on both surfaces, to 18.5 cm long and 9 cm wide, the laterals largest, the lowermost smallest and reflexed; petiolules densely yellowish-tomentose, canaliculate above, swollen apically, the laterals 15–24 mm long, the terminals 48–59 mm long. *Staminate inflorescences* axillary, branched from the base, spreading, densely yellowish-tomentose, to 19 cm long. *Staminate flowers* cream-yellow, 4-merous; pedicels sparsely yellowish-tomentose, 1.5–3 mm long; calyx broadly cupular, sparsely yellowish-tomentose, ca. 1 mm high and 2.5 mm wide, the lobes 4, acute, spreading; corolla yellowish, densely yellowish-tomentose without, pubescent within, ca. 3 mm long, the lobes 4, thick, acute, 1–1.5 mm long and ca. 1 mm wide; stamens 8, ca. as high as the corolla tube, the filaments subulate, inserted at the base of the disc between the lobes, the 4 opposite the sepals adnate basally to the corolla below the clefts, the anthers sagittate, basifixed; disc sulcate, 8-lobed, half as high as the ovary; ovary tomentose, ovoid, ca. 1 mm in diameter, half immersed in the disc, the style columnar. *Fruits* unknown.

Known only from the type collection.

BOCAS DEL TORO: Fish Creek Hills, *von Wedel 2398* (MO, holotype; F, GH, isotypes).

4. TRATTINNICKIA[3]

Trattinnickia Willd., Sp. Pl. ed. 4. 4: 887. 1805.

Trees, bark with resinous ducts. *Leaves* alternate, odd-pinnate, scattered, chartaceous to coriaceous; leaflets 5–19, opposite, acuminate apically, margins

[3]Swart, and most other botanists, have spelled this name *Trattinickia*. However, as Little (Phytologia 18: 410. 1969) has indicated, Willdenow used the spelling *Trattinnickia* in his original publication of the genus. The genus is named for the Austrian botanist Leopold Trattinnick (1764–1849), usually spelled Trattinick in the botanical literature. According to Barnhart (Biographical Notes Upon Botanists. 3: 398. 1965), "Pritzel and Neilreich spell this name Trattinick [as does F. A. Stafleu, Taxonomic Literature. 1967]; but on all his books and papers it appears invariably Trattinnick."

entire to sinuous, the laterals inequilateral basally. *Inflorescences* axillary to subterminal or terminal panicles or thryses; plants dioecious or polygamous to monoecious. *Flowers* small, 3-merous, calyx synsepalous, irregularly 3-lobed, imbricate, the lobes persistent in fruit; corolla sympetalous, fleshy, more or less tubular, 3-lobed, induplicate-valvate, inflexed-apiculate; stamens 6, the filaments short and dilated, free, inserted on the base of the disc in staminate flowers and on the disc margin in carpellate flowers; disc annular, 6-lobed; gynoecium 3-carpelled, the ovary 2–3-lobed and -loculed, fleshy, surrounded basally by the disc, abortive in staminate flowers, the ovules apical, pendulous, 2 per locule. *Fruits* drupaceous, the exocarp membranaceous, the mesocarp thick and resinous; pyrenes (1–)2, 1-seeded, corregated, thick, and woody, nearly connate, separated only by a thin layer of mesocarp; endosperm absent, the cotyledons contortuplicate.

A Neotropical, mainly South American, genus of about ten species occurring from Brazil and Peru northward to Panama and the West Indian island of St. Vincent. Two species occur in Panama. *Trattinnickia panamensis* Standley & Williams, described from Bajo Chorro, Chiriquí, is a member of the genus *Guarea* (Meliaceae). It is probably a synonym of *G. tonduzii* C. DC.

a. Leaflets scabrous, rough to the touch; inflorescences sparsely hispidulous . . . . 1. *T. aspera*
aa. Leaflets glabrous, not rough to the touch; inflorescences puberulent . . . . 2. *T. burserifolia*

1. **Trattinnickia aspera** (Standley) Swart, Rec. Trav. Bot. Néerl. 39: 426. 1942. — FIG. 5.

Protium asperum Standley, Trop. Woods 8: 4. 1926.

Trees, 15–50 m high, bark fragrant. *Leaves* scabrous, to perhaps 1.5 m long; petioles striate, canaliculate above, 8–29 cm long; leaflets 7–11(–19), ovate or ovate-lanceolate to oblong or elliptic, laterals slightly inequilateral, narrowly to broadly acuminate, cuneate to cordate basally, the margins repand to sinuous, chartaceous to coriaceous, scabridulous on both surfaces, sparingly hispidulous below, the veins more so, the lateral veins prominent below, 10–31 cm long and 4–12.5 cm wide, the middle pairs largest; petiolules hispidulous, the laterals 3–7 mm long, the terminals 29–46 mm long. *Inflorescences* axillary panicles, the peduncles and branchlets angled, striate, and sparsely hispidulous, 12–20 cm long in fruit. *Flowers* with the pedicels angled, hispidulous, 4–13 mm long in fruit, the androecium and gynoecium unknown. *Fruits* rhomboid, ridged, glabrous, acute apically, green to greenish-brown, 9–12 mm long and 8–11 mm in diameter; pyrenes 2, separated by a thin line of mesocarp, 1-seeded.

Trattinnickia aspera apparently is endemic to Panama. Known to fruit from November through April; the flowers are unknown, flowering specimens apparently never having been collected. However, the stiff scabrous leaves readily identify this species even when sterile.

BOCAS DEL TORO: Near Almirante, United Fruit Company Fruit Dale Farm, abundant, *Seibert 1589* (MO). CANAL ZONE: Barro Colorado Island, *Kenover 674* (US); wet forest, *Standley 40815* (US), *41161* (US, holotype; US, isotype), *Zetek 5088* (F, MO, US); Pearson Trail 500, *Croat 4137* (MO); Snyder-Molino Trail, *Shattuck 769* (F, MO); forest SW of Lab Clearing 100 ft N of Snyder-Molino Trail, *Croat 7674* (MO). PANAMA: Río Indio drainage ca. 9 mi. E of Transisthmian Highway, rain forest, medium slope, clay loam soil, alt. 800 ft, *Barbour 1056* (F, US).

The three areas from which this species is known are all on the Caribbean side of the Continental Divide. It apparently grows in monsoon forest and evergreen seasonal forest.

The collection *Barbour 1056* has been cited as a paratype of *Trattinnickia barbourii* Little (Phytologia 18: 410. 1969), the holotype of which is from Ecuador. However, the Panamanian collection falls under the range of variation exhibited by *T. aspera*. The Ecuadorian collection has not been seen.

Common names reported for *Trattinnickia aspera* are *caraña* (fide *Barbour 1056*) and *caraño* (fide *Standley 40815*). The labels of several collections men-

FIGURE 5. *Trattinnickia aspera* (Standley) Swart.—A. Leaf (× 3/8). B. Infructescence (× 3/8). [A, after *Croat 4137* (MO); B, after *Croat 7674*. (MO).]

tion the fragrant resin of the bark, and that on *Standley 40815* states that the tree "exudes large amounts of fragrant balsam that is gathered for market."

2. **Trattinnickia burserifolia** Mart., Nov. Gen. Sp. Pl. 3: 93. 1829.

Tree, to 30 m high; branchlets dark, puberulent, provided with lanceolate grayish lenticles. *Leaves* 18.5–28 mm long; petioles minutely puberulent, thickened basally, 3.5–7.5 cm long; leaflets 5–11, oblong to elliptic, the laterals inequilateral, abruptly acuminate, narrowly cuneate basally, the margins entire, coriaceous, glabrous, smooth and lustrous above, duller beneath, 7–12 cm long and 3–4 cm wide, the lowermost pair smallest; petiolules striate, minutely puberulent, the laterals 3–6 mm long, the terminals to 12 mm long. *Inflorescences* axillary or subterminal thryses, branched from the base, puberulent, the branches spreading, 7–13 cm long in fruit. *Flowers* with the pedicels puberulent, 2–3 mm long in fruit; "3-merous, 3–4 mm long and 2–2.5 mm in diam. Calyx cupuliform, nearly half as long as the flower; its lobes triangular, obtuse, as long as the tube. Corolla tubular, outside papillose, inside glabrous but near the apex provided with some hairs, carnose, red; its lobes ovate-triangular, acute, about as long as the tube. Stamens in the masc. fl. as long as the tube of the corolla, in the fem. fl. shorter; filaments very short, much dilated; anthers elliptic, apiculate. Disc annular, 6-lobed, glabrous, 0.25 mm high. Pistil glabrous, in the masc. fl. forming with the disc a hardly 1 mm high cone, in the fem. fl. 2 mm high; ovary conical ovoid, 1.5 mm high; stigma 2-lobed, sessile." *Fruits* globose, glabrous, the exocarp brown, thin, slightly wrinkled, 6–7 mm in diameter.

This species is known from Panama, Colombia, Venezuela, the Guianas, Brazil, and the West Indian island of St. Vincent. The single collection known from Panama is in fruit (September), and the floral description above is taken from Swart (Rec. Trav. Bot. Néerl. 39: 432. 1942).

COCLE: Region N of El Valle de Antón, alt. 1000 m, 30 m high, *Allen 3725* (F, GH, MO).

The fruits on this collection have been damaged by insects, but leaf characters definitely place it as *Trattinnickia burserifolia.*

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 121. MARCGRAVIACEAE

A. C. DEROON[1]

Lianas, vines, or shrubs, often epiphytic, with sprawling, climbing or pendulous branches. *Leaves* simple, alternate, estipulate, glabrous, mostly with hypophyllous nectariferous glands, the margins entire or minutely crenate; variously shaped sclereids frequent. *Inflorescences* terminal racemes, pseudo-umbels, or sometimes pseudo-spikes, erect or pendulous; bracts transformed into variously shaped nectaries. *Flowers* bisexual, regular, 2-bracteolate, the bracteoles sepaloid, persistent; sepals 4–5, unequal, free or nearly so, imbricate, thick and rigidly coriaceous, persistent; petals 3–5, imbricate, free or connate; stamens 3–many, the filaments free or connate basally, often adnate to the bases of the petals, the anthers 2-loculed, longitudinally dehiscent; ovary superior, competely or incompletely 2–20-loculed, the ovules mostly numerous. *Fruit* capsular, loculicidally and septifragously dehiscent from the base (or indehiscent?), the pericarp more or less woody or coriaceous, mesocarp pulpy; seeds few to numerous, with a shiny woody reticulate testa; endosperm scanty or lacking; embryo straight.

A neotropical family of four genera and about 125 species; all genera and 16 species reported from Panama.

Pollination by birds and bats as well as self-fertilization have been reported in this family.

KEY TO GENERA

a. Leaves spirally arranged; all the flowers fertile and provided with nectaries; petals reflexed at anthesis.
  b. Stamens 7–many; nectaries inserted below the middle of the pedicels. . . . 1. *Norantea*
  bb. Stamens 3–5; nectaries inserted at the middle of the pedicels or higher, mostly at the bases of the flowers.
    c. Nectaries foliaceous, slightly gibbose; ovary 2-loculed. . . . . 2. *Ruyschia*
    cc. Nectaries hollow, cup- or spur-shaped; ovary 3–5-loculed. . . . . 3. *Souroubea*
aa. Leaves distichous; the apical flowers abortive, only the nectaries developed, fertile flowers without nectaries; petals united into a deciduous cap. . . . . 4. *Marcgravia*

1. NORANTEA

Norantea Aubl., Hist. Nat. Gui. Fr. 554. 1775.

Shrubs or lianas, often sprawling, often epiphytic. *Leaves* petiolate or subsessile, the blade often coriaceous, sometimes very rigid, with a strong apical mucro or slightly retuse after the mucro is shed. *Inflorescences* racemes, spike-

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[1]Botanical Museum and Herbarium of the State University of Utrecht, Transitorium II, Heidelberglaan 2, Utrecht, Netherlands.

ANN. MISSOURI BOT. GARD. 57: 29-50. 1970.

like racemes, or umbelliformly contracted racemes; nectaries cucullate, galeate, or saccate, mostly inserted on the pedicels, mostly distant from the flower, sometimes inserted on the rachis. *Flowers* with sepaloid bracteoles, appressed to the calyx or remote; sepals 5, slightly unequal, thick, rigid, persistent; petals free or shortly connate basally or sometimes closer to the apex, reflexed at anthesis, stamens (5–)7–many, the filaments flattened, often linear, mostly free, often adnate to the bases of the petals, the anthers mostly oblong, often ± cordate basally; ovary 3–8-loculed, the ovules few to many, the stigma mostly small, often on a distinct style. *Fruit* subglobose, apiculate through the persistent style and stigma; seeds shining, reticulate.

A genus of about 35 species, three species being recorded from Central America, of which two are known from Panama. The species placed in this genus form a rather heterogeneous assemblage so that it is not impossible that the genus may be split in the future.

a. Inflorescences umbelliform, the rachis 0.5–2 cm long . . . . . 1. *N. subsessilis*
aa. Inflorescences racemose, the rachis 4–7 cm long . . . . . 2. *N. costaricensis*

1. **Norantea subsessilis** (Benth.) Donn. Sm., Bot. Gaz. (Crawfordsville) 24: 390. 1897.—Fig. 1.

Ruyschia subsessilis Benth., Bot. Voy. Sulphur 73. 1844.
Norantea albido-rosea Gilg, Bot. Jahrb. Syst. 42: 126. 1909.

Epiphytic *shrub* or liana; branchlets stout, terete or subterete, yellowish-brown to dark reddish-brown when dried, grayish with age. *Leaves* subsessile or shortly petiolate, the petioles stout, 3–7 mm long and 2–4 mm wide, flattened or canaliculate above; blade obovate, obovate-oblong, or oblong, often slightly asymmetric, (1.5–)2–3 times as long as wide, 4–12 cm long and 2.5–5 cm wide, obtuse, rounded, or rarely subacute apically, obtuse, rounded, or truncate and sometimes subcordate basally, the midrib prominent beneath, the lateral veins sometimes visible above, mostly slightly prominent or sometimes obscure beneath; hypophyllous glands small but mostly conspicuous, the pore with a narrow pale circumvallation, mostly few, (1–)2–5 on either side of the midrib in the apical half of the blade, the largest in or just below the middle of the blade and 3–6 mm from the revolute margin, the others smaller and closer to the margin, two glands at the base near the midrib. *Inflorescences* umbelliform, with 10–20 flowers, the rachis 0.5–1.5 cm long, erect; nectaries saccate, erect when young, afterwards pendulous, curved, 1–2 cm long, sessile, inserted 0.5–2 cm from the base of the pedicel, the opening rounded, with a narrow, sometimes slightly revolute rim. *Flowers* large, the pedicels 4–7 cm long, shrivelled and 1.5–3 mm thick when dried; bracteoles triangular-ovate, 3–4 mm long and 3–5 mm wide; sepals suborbicular, ca. 4–5 mm long and 4–7 mm wide; petals coriaceous, connate for ca. ⅔ of their length, the tube ca. 6–10 mm long, the lobes ca. 5 mm long and ca. 5 mm wide, at anthesis the tube ruptured and the lobes reflexed; stamens ca. 35–40, the filaments filiform, ca. 5 mm long and 0.5 mm wide, the anthers oblong or lanceolate-oblong, ca. 3 mm long and ca. 1 mm wide; pistil flask-shaped, ca. 8 mm long, the ovary (3–)4-loculed, ca. 5 mm in diame-

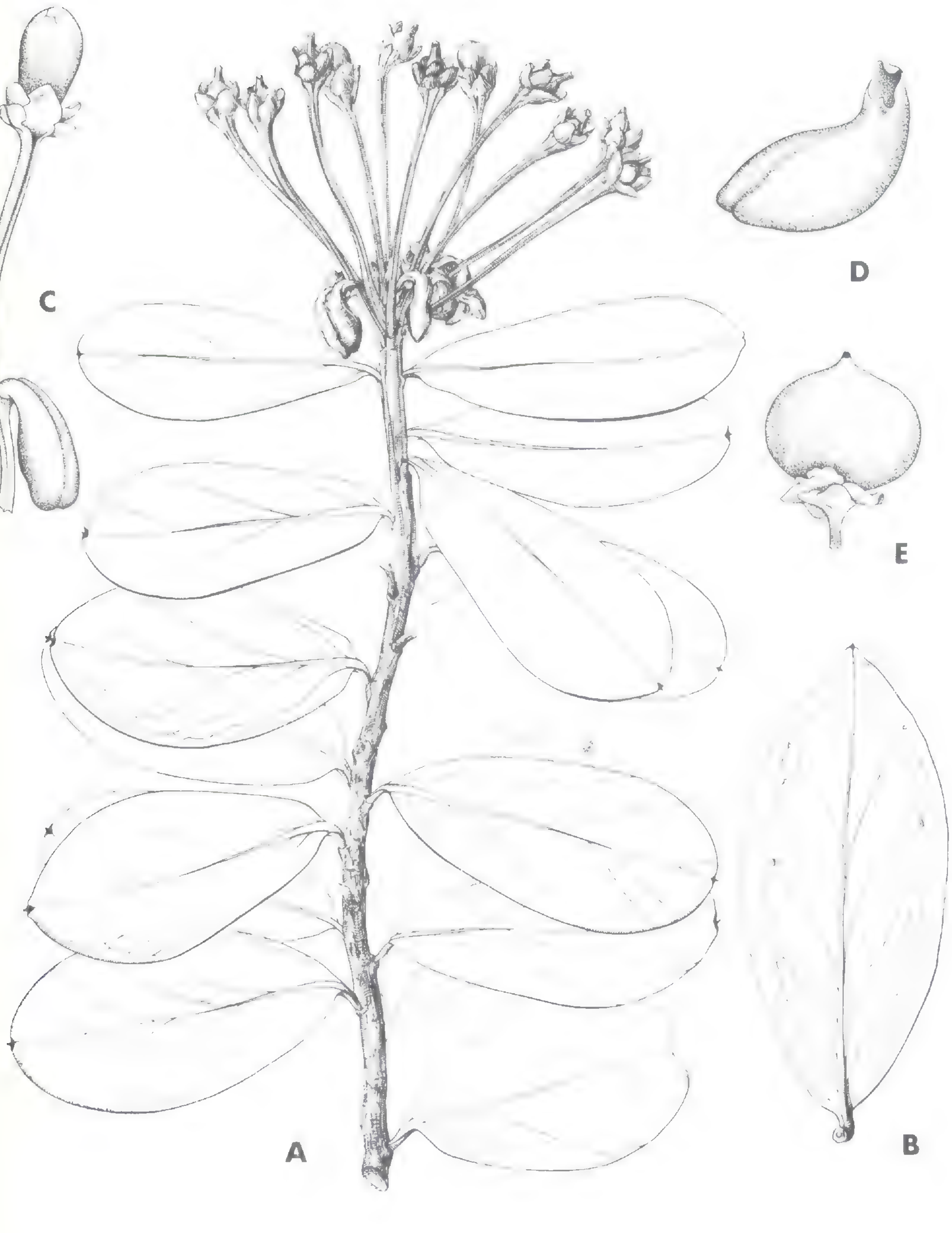

FIGURE 1. *Norantea subsessilis* (Benth.) Donn. Sm.—A. Habit (× 2/3).—B. Leaf, abaxial view (× 2/3).—C. Flower with pedicel and nectary (× 1).—D. Nectary (× 1 2/3).—E. Fruit (× 1). [A, after *Allen 2161* (F); B–D, after *Tonduz 13108*, Costa Rica (US); E, after *Allen 3740* (MO, NY, S, US).]

ter, the style ca. 3 mm long. *Fruit* subglobose, apiculate, 1–1.5 cm long and 1.5–2 cm wide, reddish, woody.

Costa Rica, Panama, and Colombia.

BOCAS DEL TORO: Without locality, *von Wedel 392* (MO). Region of Almirante, Bocas Island, *Cooper 467* (F, NY); Cricamola Valley, *Cooper 467a* (F, NY). Vicinity of Chiriqui Lagoon, Old Bank Island, *von Wedel 2035* (GH). Isla Colón, *von Wedel 107* (MO). COCLE: Hills N of El Valle de Antón, alt. 1000 m, *Allen 2161* (F, NY). Region N of El Valle de Antón, alt. 1000 m, *Allen 3740* (MO, NY, S, US). PANAMA: Cerro Campana, alt. 3000 ft, *Duke 10731* (MO). Tocumen area, *Dwyer et al. 7249* (MO).

2. **Norantea costaricensis** Gilg, Bot. Jahrb. Syst. 25, Beibl. 60: 31. 1898.—FIG. 2.

Epiphytic shrub or vine, the branchlets rather stout, yellowish-brown to dark brown when dried, becoming grey with age. *Leaves* short-petiolate or subsessile, the petiole stout, 2–6 mm long and 2–4 mm wide, flattened or canaliculate above; blade obovate-oblong or obovate, mostly ca. 2 times as long as wide, 6–11 cm long and 2.5–4.5 cm wide, obtuse to rounded and mucronate apically or often slightly retuse after the mucro is shed, narrowed and rounded basally; coriaceous, the midrib subprominent to sulcate above, prominent beneath, the lateral veins obscure on both sides of the blade or prominent beneath; hypophyllous glands small, in a row of mostly 10–17 or sometimes less and ca. 4–8 mm from the revolute margin, mostly conspicuous, often also visible on the upper side of the blade. *Inflorescences* 6–20-flowered racemes, the rachis 4–7 cm long; nectaries cymbiform, ca. 1–1.7 cm long and 0.5–1 cm wide, reddish, inserted 0.5–2 cm from the base of the pedicel. *Flowers* large, the pedicels 4–7 cm long and ca. 2 mm thick, thickened apically and basally; bracteoles suborbicular to semiorbicular, 3–7 mm wide and 3–6 mm long; sepals suborbicular, often truncate-rotundate basally, ca. 4–7 mm long and ca. 4–8 mm wide; petals free, obovate-elliptic, ca. 10–12 mm long and ca. 5–6 mm wide, thick, reflexed, reddish; stamens 10–20(–30), mostly ca. 18, the filaments flattened, ca. 6 mm long and ca. 1.5 mm wide, adnate to the bases of the petals, the anthers elliptic-oblong, ca. 3 mm long and 1.5–2 mm wide, cordate basally, the pollen purplish-red; pistil flask-shaped, the ovary ca. 4 mm high and ca. 3–5 mm in diameter, 4-loculed, the style to 3 mm long, ca. 1 mm thick. *Fruit* globose, apiculate, irregularly dehiscent from the base, mesocarp pulpy.

Known from Costa Rica and Panama; alt. 1500–2500 m.

CHIRIQUI: Vicinity of Bajo Mona and Quebrado Chiquero, alt. 1500 m, *Woodson & Schery 587* (F). Vicinity of Cerro Punta, *Allen 3510* (G-DEL, MO, S). Upper Chiriquí Viejo Valley, vicinity of Monte Lirio, *White 40* (F, GH, MO).

2. RUYSCHIA

Ruyschia Jacq., Enum. Syst. Pl. Carib. 2. 1760.

Shrubs, often epiphytic, or vines. *Leaves* coriaceous, often rigid. *Inflorescences* terminal multiflorous racemes; nectaries small, to 5 mm long, mostly solid and gibbose to subglobose, mostly inserted at the base of the flowers. *Flowers* often fragrant, short-pedicellate; bracteoles sepaloid, appressed to the calyx, persistent; sepals 5, slightly unequal, persistent; petals free or shortly united basally, reflexed at anthesis; stamens 5 or 3, the filaments flattened, ± adnate to the bases of the petals, the anthers ovate to globose; ovary 2-loculed, ovules to ca. 20 per

FIGURE 2. *Norantea costaricensis* Gilg.—A. Habit (× 3/5).—B. Flower (× 1⅕).—C. Nectary (× 1⅘). [After *Skutch 3441*, Costa Rica (NY).]

locule, the stigma small, style usually short. *Fruit* subglobose, ± woody, apiculate, probably dehiscent; seeds few, shining, reticulate.

A genus of seven species in Central America, the Lesser Antilles, Venezuela, Colombia, and Peru; three species have been reported from Central America, of which only one is known from Panama.

1. **Ruyschia phylladenia** Sandwith, Kew Bull. 1930: 153. 1930.

Climbing epiphytic or terrestrial *shrub* or vine, the branchlets slender, smooth, becoming gray with age. *Leaves* small, the petiole 2–5 mm long; blade oblanceolate or rarely obovate or lanceolate, 2.5–4 times as long as wide, 4–9.5 cm long and 1.5–3 cm wide, acute or subobtuse or sometimes subacuminate apically, acute or subtruncate basally, thinly coriaceous, the midrib flat above, prominent beneath, the lateral veins hardly visible or hidden; hypophyllous glands mostly few (3–9) and several mm from the revolute margin or absent, large, with a thick circumvallation. *Inflorescences* many-flowered racemes, 7–15 cm long; nectaries foliaceous, spathulate, flat, slightly gibbose, 4–5 mm long and ca. 2 mm wide, the apex acute, inserted at the middle of the pedicels or higher, occasionally close to the base of the flowers. *Flowers* with slender pedicels, (5–) 7(–9) mm long; bracteoles to 2 mm long and to 1.5 mm wide, appressed to the calyx; sepals suborbicular, 1.5–2.5 mm long and 2–3 mm wide; petals obovate-oblong, ca. 7 mm long and ca. 3 mm wide, free or nearly so, reflexed; stamens 3, the filaments flattened, ca. 4 mm long and ca. 1 mm wide basally, narrowed apically, adnate to the bases of the petals, the anthers ovate-subglobose, to 1 mm long and ca. 0.75 mm wide; ovary globose, ca. 2 mm in diameter, the style 1.5 mm long. *Fruit* globose, ca. 5 mm in diameter, apiculate, cherry-pink.

Known from Costa Rica and Panama; collected at altitudes of 800–1400 m.

CHIRIQUI: Boquete, *Davidson* 824 (F, GH).

3. SOUROUBEA

Souroubea Aubl., Hist. Pl. Gui. Fr. 244. 1775.

Lianas or sprawling shrubs, sometimes epiphytic. *Leaves* petiolate, chartaceous or coriaceous. *Inflorescences* racemes; nectaries hollow, tubular, horn-shaped, or clavate, often auriculate, inserted at the bases of the flowers. *Flowers* often fragrant, pedicellate; bracteoles appressed to the calyx, persistent; sepals 5, slightly unequal, persistent; petals 5, rarely 3, free, from shortly connate basally to connate throughout nearly their whole length, reflexed at anthesis; stamens 5 or 3, the filaments flattened, wide, often connate basally and often abruptly narrowed apically, often adnate to the bases of the petals, the anthers ovate to subglobose; ovary incompletely (3–)5-loculed, often pentagonal, the stigma sessile, mostly large and radially 5-lobed. Fruit subglobose, the pericarp often very thick, woody, apiculate through the persistent stigma, the mode of dehiscence unknown; seeds rather few, shining, reticulate.

A genus of about 20 species in tropical America; six species are reported from Central America, of which five are known from Panama.

a. Inflorescences dense, the flowers small; nectaries tubular, auricles shorter than the spur or absent.
  b. Stamens 3; pedicels 3–5 mm long ..... 1. *S. loczyi* ssp. *minima*
  bb. Stamens 5; pedicels 6–18 mm long.
    c. Corolla lobes cordate ..... 2. *S. venosa*
    cc. Corolla lobes not cordate ..... 3. *S. gilgii*

aa. Inflorescences lax, the flowers relatively large; nectaries clavate, auriculate, the auricles ca. as long as the spur.
d. Leaves chartaceous; petals connate (before anthesis) for at least half their length ..... 4. *S. sympetala*
dd. Leaves coriaceous; petals free or only connate basally ..... 5. *S. vallicola*

1. **Souroubea loczyi** ssp. **minima** de Roon, Acta Bot. Neerl. 18: 200. *pl.* 3. 1969.

Norantea loczyi Al. Richter, Math. Természettud. Értes. 34: 816. 1916.
Souroubea triandra Lundell, Phytologia 1: 244. 1937.

Epiphytic *shrub,* the branchlets slender, grayish. *Leaves* (sub-)coriaceous, the petioles 4–10 mm long and 1–2 mm wide, canaliculate above; blades elliptic-oblong to obovate-oblong, 2–2.5 times as long as wide, 5–8.5 cm long and 2–3.5 cm wide, obtuse to rounded or sometimes subacute apically, cuneate or nearly so basally, the midrib sulcate apically and prominent basally above, prominent beneath, the lateral veins hidden to subprominent above, prominent beneath; hypophyllous glands minute, variable in number, in a row 3–7 mm from the revolute margin. *Inflorescences* multiflorous racemes, the rachis 8–12 cm long; nectaries horn-shaped, 3–5 mm long and 1–2 mm in diameter, minutely auriculate, the auricles 1–1.5 mm long. *Flowers* small, the pedicels 3–5 mm long; bracteoles ovate to semi-orbicular; sepals semi- to suborbicular, ca. 1 mm long and ca. 1.5 mm wide; corolla gamopetalous, 3-lobed, the tube ca. 1.5 mm long in bud, at anthesis ruptured and the lobes ca. 1.5 mm long, reflexed; stamens 3, the filaments free, flattened, ca. 1.5 mm long, the anthers ovate-globose, ca. 1 mm long; ovary 3-loculed, ovoid, ca. 1.5 mm long, ca. 1 mm in diameter, the stigma 3-lobed. *Fruit* globose, ca. 5 mm in diameter, apiculate.

Known from Costa Rica and Panama. The ssp. *loczyi* is known from Mexico, Guatemala, and British Honduras.

COCLE: North rim of El Valle, *Allen 1914* (MO).

2. **Souroubea venosa** Schery, Ann. Missouri Bot. Gard. 27: 320. 1940.—FIG. 3.

Epiphytic *shrub* or liana, the main stems to 10 cm thick, the branches and branchlets becoming gray with age. *Leaves* chartaceous to thinly coriaceous, the petioles 2–6 mm long and 1.5–3.5 mm wide, flattened or slightly canaliculate above; blades elliptic, elliptic-oblong, or obovate, 1.5–2.5 times as long as wide, 7–15 cm long and 3.5–9 cm wide, obtuse or rounded or sometimes slightly acuminate apically, cuneate or sometimes subobtuse basally; the midrib slightly prominent above, prominent beneath, the lateral veins and the veinlets prominent, at least beneath, hypophyllous glands small, numerous, in a usually distinct row 3–10(–15) mm from the margin. *Inflorescences* multiflorous racemes, the rachis 10–15 cm long; nectaries tubular, straight or slightly curved, with a more or less conspicuous longitudinal groove, 5–8 mm long, 1–1.5 mm in diameter, the apex often globose, the orifice with a subauriculate rim. *Flowers* small, fragrant, the pedicels 6–12 mm long and to ca. 1 mm in diameter; bracteoles suborbicular, ca. 1 mm long and ca. 2 mm wide; sepals suborbicular, 1–1.5

mm long and 2–2.5 mm wide; corolla gamopetalous, 5-lobed, the tube 2–2.5 mm long and ca. 2 mm in diameter, the lobes cordate, ca. 2 mm long and 2–3 mm wide, the apex rounded; stamens 5, the filaments flattened, 3–3.5 mm long, ca. 1 mm wide at the base, narrowed apically, the anthers ca. 1 mm long; ovary ovate, ca. 2 mm long and ca. 1.5 mm in diameter, 5-loculed, the stigma large, radially 5-lobed. *Fruit* not seen.

Known from Panama only. Forms dense growths on trees in moist forests and thickets in regions having a dry season. On San José Island along streams and on wooded coastal cliffs; here the leaves are shed in February and renewed in late March before the abundant flowering in April and early May. On the mainland also collected in flower from June to August. Alt. to 700 m.

COCLE: El Valle de Antón, S rim, alt. 700 m, *Allen* 3537 (C, F, FI, G-DEL, MICH, MO, NY, S, U, UC, US). Between Las Margaritas and El Valle de Antón, *Woodson et al. 1289* (F, GH, NA, NY). PANAMA: Between Pacora and Chepo, boggy grasslands and marginal thickets, alt. 25 m, *Woodson et al. 1652* (F, GH, NA, NY). Savana de Alhajuela, Chagres Valley, *Pittier 3466* (US). San José Island, Punta del Cabo, coastal bluff, *Erlanson 80* (GH, NA, NY, US); canyon N of Red Hill, *Johnston 692* (GH); South Beach, *Johnston 1093* (GH). VERAGUAS: Santiago, 4 mi. from Panamerican Highway toward Atalaya, *Dwyer & Kirkbride 7417* (MO).

3. **Souroubea gilgii** Al. Richter, Math. Természettud. Értes. 34: 835. 1916.

S. belizensis Lundell, Field & Lab. 13: 8. 1945.

Climbing epiphytic *shrub* or liana. *Leaves* large, chartaceous, short-petiolate or subsessile, the petiole 2–5 mm long and 2–3 mm wide, flattened or canaliculate above; blade obovate-oblong, 2–2.5 times as long as wide, 11–17 cm long and 4.5–7.5 cm wide, often conspicuously asymmetric, acute to obtuse apically, the base cuneate and often slightly rounded at the petiole; the midrib sulcate to prominent above, prominent beneath, the lateral veins prominent or slightly prominent beneath; hypophyllous glands small or minute, mostly numerous and in (1–)2(–3) often inconspicuous and irregular rows at varying distances from the margin, mostly a row 5–8(–12) mm from the margin and a row of more numerous and smaller glands 0.5–2(–3) mm from the margin. *Inflorescences* dense, multiflorous racemes, the rachis 10–20 cm long, puberulent; nectaries tubular, 7–15 cm long, 1–2 mm in diameter, the opening with a short auriculate rim, the auricles to 5 mm long and 2 mm wide, the apex subglobose. *Flowers* small, the pedicels 10–18 mm long, ca. 1 mm in diameter; bracteoles ovate-suborbicular, 2–3 mm long and 2–3 mm wide; sepals broadly suborbicular, 2–4 mm long and 3.5–5 mm wide; corolla gamopetalous, ca. 8 mm long, the tube ca. 4 mm long and ca. 4 mm in diameter, the lobes in bud ca. 3 mm long, at anthesis the tube ruptured and the lobes ca. 5 mm long, reflexed; stamens 5, the filaments flattened, ca. 5 mm long, ca. 2 mm wide basally, narrowed apically, the anthers ovate-subglobose, 1–1.5 mm long; ovary ovate, 5-ribbed, ca. 2.5 mm long, 5-loculed, the stigma large, radially 5-lobed. *Fruit* not seen.

Rainforests of Atlantic Central America from British Honduras to Panama. Low altitudes.

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, alt. 10–50 m, *Woodson et al. 1899* (F, GH, MO, NA, NY).

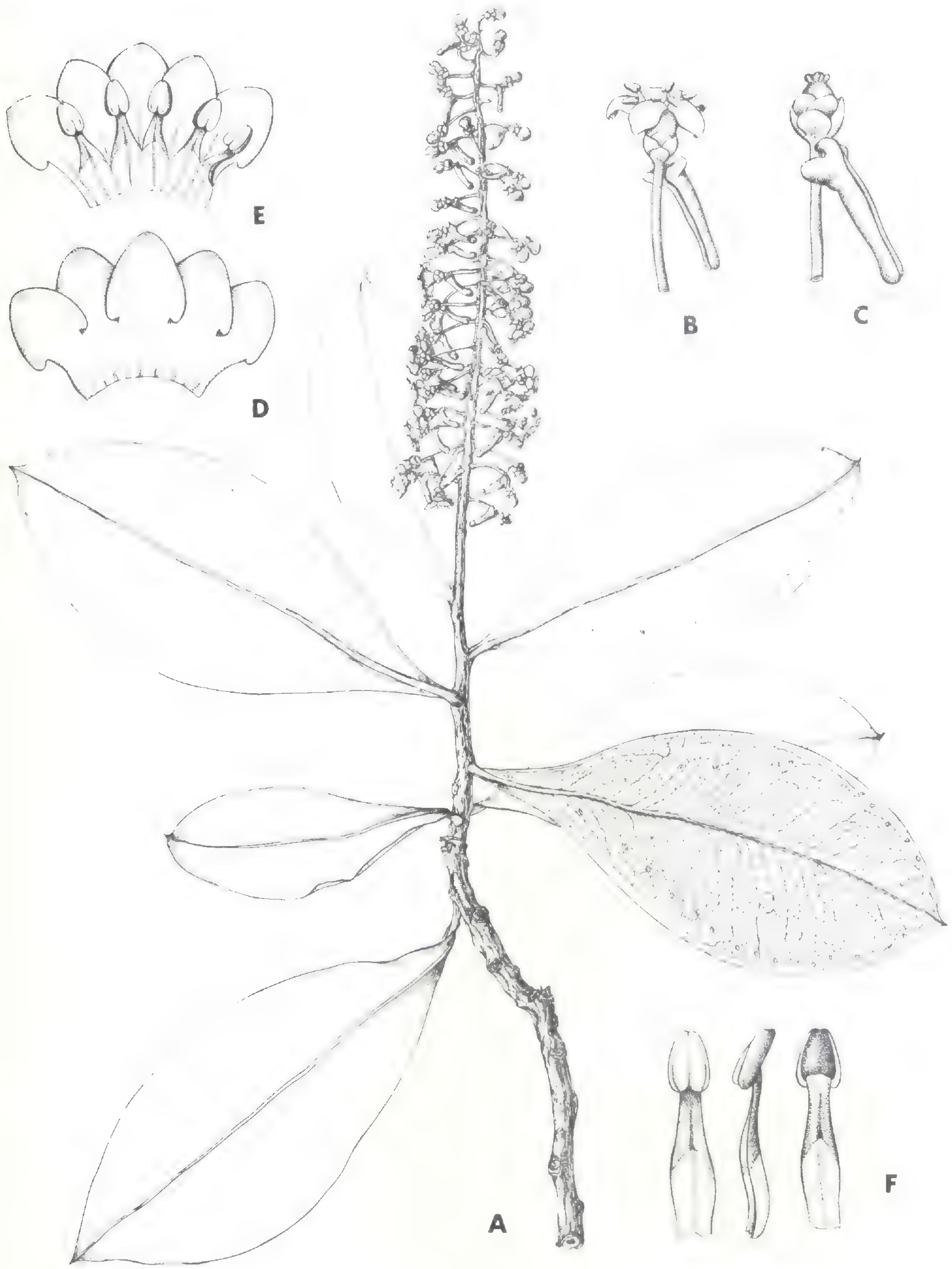

FIGURE 3. *Souroubea venosa* Schery.—A. Habit (× 3/5).—B. Flower with nectary (× 2 2/5).—C. Flower with corolla shed (× 2 2/5).—D. Corolla, outside (× 3 3/5).—E. Corolla with stamens (× 3 3/5).—F. Stamens (× 7 1/5). [After *Allen* 3537 (UC).]

4. **Souroubea sympetala** Gilg, Bot. Jahrb. Syst. 25, Beibl. 60: 32. 1898.

Liana or scandent shrub, sometimes epiphytic, the stems with numerous long aerial roots, the branchlets yellowish or grayish-white to yellowish-brown or dark gray, the older branches with dark silvery gray bark. *Leaves* variable in shape and size, often asymmetric, chartaceous when dried; petiole 5–12(–20) mm long and 1.5–2.5 mm wide, canaliculate above; blade elliptic-oblong, oblong, obovate-oblong, or rarely lanceolate or obovate, (1.5–)2(–3) times as long as wide, 8–14(–16) cm long and 3.5–6(–8) cm wide, subacute, obtuse, or rounded, or sometimes acute or subacuminate apically, acute to obtuse or sometimes rounded basally; the midrib flat to slightly prominent and often sulcate above, prominent beneath, the lateral veins mostly prominent on both sides of the blade; hypophyllous glands variable in number and size, from small (0.5 mm) and inconspicuous to large (ca. 2 mm) and conspicuous, often 4–15 in a more or less distinct and regular row 5–12 mm from the margin and often another row of smaller glands near the margin, especially in the apical part of the blade, rarely completely or almost wanting. *Inflorescences* lax, mostly with 15–30 flowers, the rachis 10–30 cm long, yellowish-brown puberulent, often rugose when dried; nectaries auriculate spurs, straddling the pedicels, 15–33 mm long, the spur clavate, 7–15 mm long, the auricles 10–20 mm long and 2–5 mm wide. *Flowers* fragrant, the pedicels slender to stout, especially in fruit, from 1 cm at the apex of the inflorescence to 2–4(–5.5) cm long at the base, 1–2 mm thick, puberulent, often dark and finely wrinkled when dried; bracteoles semi- to suborbicular, 2–2.5 long and ca. 3 mm wide; sepals suborbicular, 2–3 mm long and 3–4.5 mm wide; corolla gamopetalous, the petals mostly connate for more than half their length, 7–11 mm long, at anthesis the tube ruptured and the lobes reflexed; stamens 5, the filaments flattened, 4–6 mm long, 2–3 mm wide, connate basally, narrowing apically, the anthers ovate, 1.5–2.5 mm long and 1–1.5 mm wide; ovary 5-loculed, pentagonal, ca. 2.5 mm long and 2–3 mm in diameter, the stigma large, 5-radiate. *Fruit* globose, hard and woody when dried, ca. 2 cm in diameter, apiculate.

Known from British Honduras, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, and northeastern Peru; tropical rain forests, below 1000 m.

BOCAS DEL TORO: Without locality, *von Wedel 461* (GH, MO). Vicinity of Chiriquí Lagoon, Fish Creek Lowlands, *von Wedel 2391* (GH, MO); Old Bank Island, *von Wedel 1963, 2107* (both GH, MO), *2140* (GH); Water Valley, *von Wedel 1661, 1842* (both GH, MO), *2665* (MO). CANAL ZONE: Barro Colorado Island, *Aviles 9b* (F), *Bailey 544* (F), *M. Brown 117* (F), *Shattuck 503* (MO); near Drayton House, *Woodworth & Vestal 552* (F, GH); shore at French Lock Site, *Zetek 4341* (MO); lake shore W of Laboratory, *Hayden 83* (MO); Pena Blanca Point, *Shattuck 804* (F, MO); Wheeler Trail, *Starry 96* (F); Zetek Trail, *Shattuck 513* (F). Chagres, *Fendler 291* (GH, LE, MO, P, US, W). Near Gatun, *Hayes 345* (NY, US), *Wagner s.n.* (M). In swamp near Gatún Bridge, *Hayes s. n.* (F, GH, US). Quebrada Culebra, *Steyermark s. n.* (G-DEL). Westerly arm of Quebrada Salamanca, *Dodge et al. 17003* (FI, G-DEL, MICH, MO, S, U). Río Medio, *Miller 1759* (US). COLON: Swamps near Fort San Lorenzo, *Allen 3433* (G-DEL, MO, S). PANAMA: Vicinity of La Chorrera, *Allen 4264* (G-DEL, MO, NY).

The following names have been misapplied to this species:
Ruyschia bicolor Hemsley, Biol. Centr.-Amer., Bot. 1: 92. 1879, non Benth., 1844.
Ruyschia lepidota Hemsley, Biol. Centr.-Amer., Bot. 1: 92. 1879, non Miq., 1843.
Souroubea guianensis Standley, Contr. U. S. Natl. Herb. 27: 266. 1928; Standley, Contr. Arnold Arbor. 5: 107. 1933, non Aubl., 1775.

5. **Souroubea vallicola** Woodson *ex* de Roon, Acta Bot. Neerl. 18: 200. 1969. —FIG. 4.

Climbing *shrub* or liana, often epiphytic; branchlets stout, sometimes tortuous, becoming gray with age. *Leaves* coriaceous, rigid, the petiole 4–10 mm long and 2–3 mm wide, canaliculate above; blade obovate, 1.5–2 times as long as wide, 6–13 cm long and 3–7 cm wide, rounded or obtuse, mucronate when young, afterwards mostly slightly retuse apically, acute or sometimes obtuse basally, the midrib flattened or slightly prominent above, prominent beneath, the lateral veins prominent beneath, the margin revolute; hypophyllous glands absent or only a few small and hardly visible ones near the margin. *Inflorescences* short, 15–22 flowered racemes, the rachis 4–12 cm long, ferrugineous-puberulent; nectaries auriculate spurs, the spur clavate, 7–10 mm long, the auricles 8–12 mm long. *Flowers* with puberulent pedicels, 1–2 cm long; bracteoles suborbicular, 2–4 mm long and 2–4 mm wide; sepals suborbicular, 3–5 mm long and 4–6 mm wide; petals obovate-oblong, 7–10 mm long and 4–5 mm wide, connate basally; stamens 5, the filaments flattened, 5–6 mm long, ca. 1 mm wide basally, narrowed apically, free or connate basally, the anthers ovate, 1.5–2 mm long and 1–2 mm wide; ovary pentagonal, 5-loculed, ca. 3–4 mm long and ca. 2–3 mm in diameter, the stigma large, radially lobed. *Fruit* unknown.

Known from Panama and Costa Rica.

COCLE: El Valle de Antón, North Hills, alt. 1000 m, *Allen 3541* (C, F, FI, G-DEL, MO, NY, S, U, UC, US).

4. MARCGRAVIA

Marcgravia L., Sp. Pl. 503. 1753.

Climbing *shrubs* or vines, often epiphytic, with dimorphic branches and leaves; the sterile, juvenile branches creeping, appressed to the substrate, and attached by roots; the fertile branches free, mostly pendulous, often angular, and provided with wartlike lenticels. *Leaves* distichous, those of the sterile, creeping branches small, thin, sessile, mostly cordate; those of the fertile branches dimorphic, larger and thicker, often with a drip-tip. *Inflorescences* mostly umbelliform, sometimes racemose, the apical (central) flowers abortive with only the bracts (nectaries) well-developed, the fertile flowers without bracts. *Flowers* pedicellate, the bracteoles sepaloid, mostly appressed to the calyx; sepals 4, decussate, the inner 2 smaller, persistent; petals connate into a deciduous cap; stamens 7–many, free; ovary 4–20-loculed, the ovules numerous. *Fruit* capsular, mesocarp pulpy, often loculicidally and septifragally dehiscent from the base; seeds numerous.

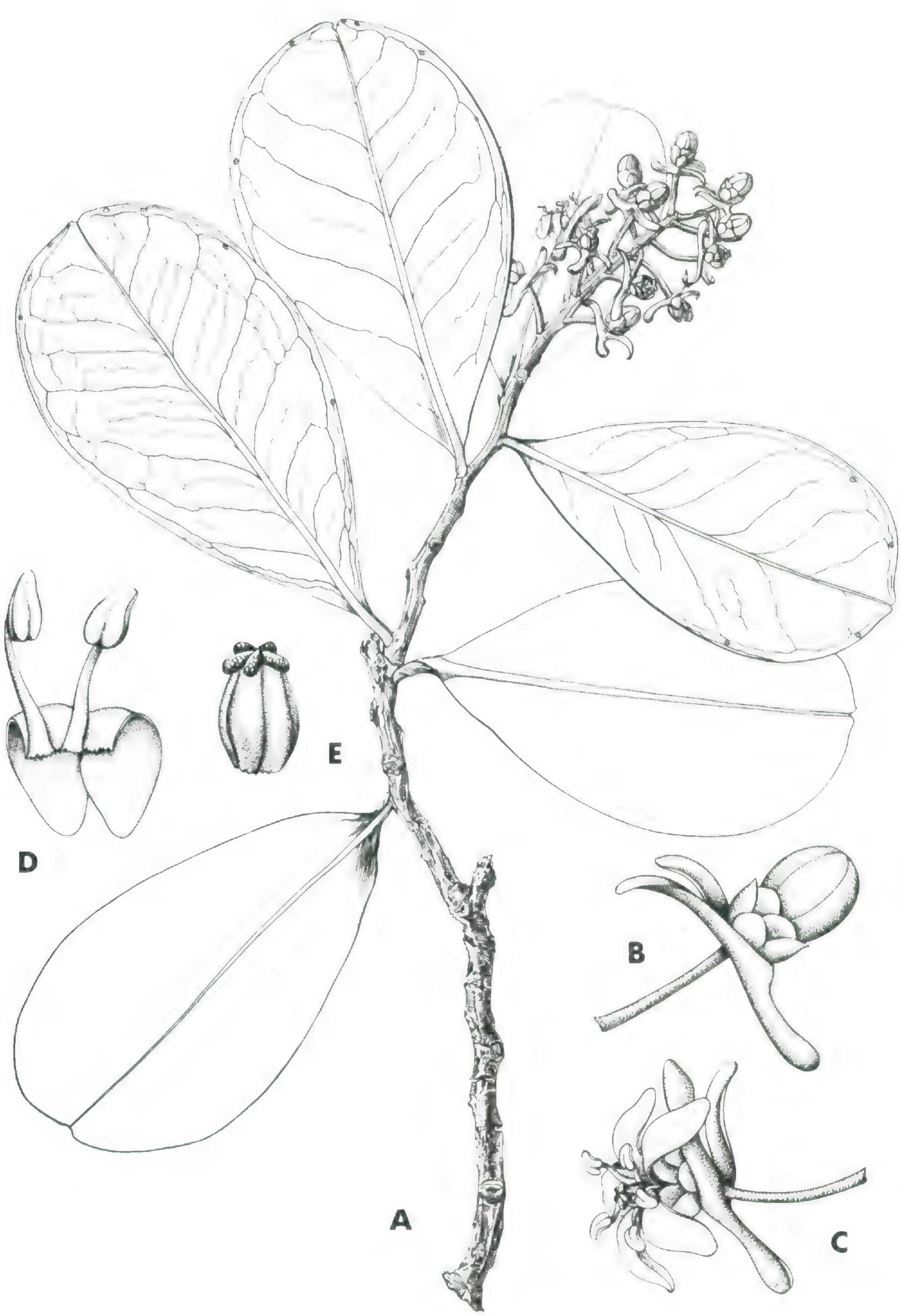

FIGURE 4. *Souroubea vallicola* Woodson *ex* de Roon.—A. Habit (× ¾).—B. Flower with nectary (× 2).—C. Flower at anthesis (× 2).—D. Petals with stamens (× 4).—E. Ovary with stigma (× 4). [After *Allen 3541* (U).]

A genus of about 60 species; about 12 species in Central America, of which eight are known from Panama.

An important character within the genus *Marcgravia* is how the flowers are inserted on the pedicels. In the existing literature the descriptions of this character are inaccurate and often even misleading. There are three possibilities which may be characterized as "flowers erect on pedicels" (Fig. 5B), "flowers oblique on pedicels" (Fig. 7B), and "flowers perpendicular on pedicels" (Fig. 8B). This is the terminology I have used for *Marcgravia* in the key to species and in the descriptions of the various species.

a. Flowers erect or oblique on pedicels; nectaries pitcher-shaped, 1.5–5 cm long.
  b. Leaves 1.5–5.5 cm wide; pedicels 2–7 cm long.
    c. Pedicels 3.5–7 cm long.
      d. Lateral veins and veinlets more or less prominent on both sides of the blade; nectaries much shorter than the pedicels.
        e. Leaves with numerous dark dots below . . . . . 1. *M. serrae*
        ee. Leaves without dark dots . . . . . 2. *M. macrophylla*
      dd. Lateral veins and veinlets (mostly) obscure; nectaries only a little shorter than the pedicels.
        f. Inflorescence with 15–30 flowers and 3–5 nectaries . . . . 3. *M. brownei*
        ff. Inflorescence with 7–12 flowers and only one nectary or none . . . . . 4. *M. schippii*
    cc. Pedicels 2–3 cm long . . . . . 5. *M. affinis*
  bb. Leaves 5–10 cm wide; pedicels ca. 1.5 cm long.
    g. Leaves membranaceous, not punctate below . . . . . 6. *M. membranacea*
    gg. Leaves rigidly coriaceous, punctate below . . . . . 7. *M. atropunctata*
aa. Flowers perpendicular on pedicels; nectaries dipper-shaped, 5–7.5 cm long . . . . . 8. *M. nepenthoides*

1. **Marcgravia serrae** de Roon, Acta Bot. Neerl. 18: 197. *pl. 1*. 1969.—Fig. 5.

Climbing epiphytic *shrub* or vine, the flowering branchlets quadrangular, with rows of lenticels. *Leaves* shortly petiolate, the petiole 2–5 mm long; blade oblanceolate-oblong, obovate-oblong, or sometimes elliptic-oblong, 3–4 times as long as wide, 7–14 cm long and 2–4.5 cm wide, abruptly acuminate apically, the acumen 1–2 cm long, attenuate or acute basally, chartaceous to thinly coriaceous, the midrib prominent beneath, the lateral veins prominent or slightly prominent on both sides of the blade, the veinlets mostly prominent; hypophyllous glands various, a row of minute dark glands along the margin, numerous minute dark punctiform scattered glands, and sometimes (1–)3–5 small poriform glands in an oblique row in the basal part of the blade. *Inflorescences* umbelliform, with (20–)30–45 fertile flowers and 3–5 nectaries, the rachis ca. 1 cm long; nectaries urceolate, stalked, the stalk 5–8 mm long, the cup 1–2 cm long and ca. 4–5 mm in diameter, with a rudimentary bud near the apex, the orifice large, rounded, with an often revolute and apiculate rim. *Flowers* erect on the pedicels; the pedicels 3.5–5 cm long, to 7 cm long in fruit, lenticellate, scurfy; bracteoles ca. 1 mm long and 2–3 mm wide; sepals broadly suborbicular or reniform, ca. 2–3 mm long and 4–5 mm wide; corolla oblong-subconical, ca. 1 cm long and 4–6 mm in diameter; stamens 18–35, the filaments flattened, unequal, 4–6 mm long in bud, the anthers 3–5 mm long and ca. 1 mm wide; ovary ca. 2–3 mm in diameter, including the short style ca. 4 mm long, 6–11-loculed.

FIGURE 5. *Maregravia punctata* de Roon. A. Habit (× 1/2). B. Flower (× 2).—C. Nectary (× 1¼).—D. Transitional form between fertile flower without bract and nectary (bract) with rudimentary bud (× 1). [After Skutch 3762, Costa Rica (US).]

Fruit globose, ca. 9 mm in diameter, apiculate.

Known from Costa Rica and Panama; epiphytic in montane rainforests, alt. 1500–2500 m.

CHIRIQUI: Boquete district, Bajo Chorro, alt. 6000 ft, *Davidson* 398 (GH, US); Cerro Horqueta, dense woodland in cloud forest, alt. 5000–6000 ft, *Dwyer & Hayden* 7708 (GH, MO). Premontane rainforest (oak forest) between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke* 899 (MO). Cloud forest between Quebrada Hondo and divide on Caldera, Chiriquiciot, *Kirkbride & Duke* 929A (MO).

2. **Marcgravia macrophylla** (Wittmack) Gilg, Bot. Jahrb. Syst. 25, Beibl. 60: 27. 1898.

Large *vine,* the flowering branchlets angular or compressed, lenticellate. *Leaves* large, petiolate, the petiole ca. 5 mm long, canaliculate above; blade oblong, 2.5–4 times as long as wide, (8–)12–17 cm long and (3–)4–5.5 cm wide, acuminate apically, the acumen 1–1.5 cm long, obtuse to acute basally, coriaceous, the midrib slightly prominent apically and sulcate basally above, prominent beneath, the lateral veins (slightly) prominent on both sides of the blade, the veinlets prominent or slightly prominent; hypophyllous glands numerous, inconspicuous, a row of minute dark glands in the margin and a row of minute poriform glands, not or hardly visible with the unaided eye, 3–10 mm from the margin. *Inflorescences* umbelliform, with ca. 20(–40?) flowers and 1–3 nectaries, the rachis ca. 1 cm long; nectaries urceolate, 2–3.5 cm long, the stalk 5–10 mm long, the cup 1.5–2.5 cm long, ca. 5 mm wide at the orifice, the inflated part to ca. 1 cm wide. *Flowers* erect on the pedicels; the pedicels 3.5–5 cm long, to 7 cm long in fruit, lenticellate, scurfy; bracteoles broadly suborbicular to reniform, ca. 2 mm long and 3–4 mm wide; sepals suborbicular to reniform, ca. 3 mm long and ca. 5–6 mm wide, the margin ciliate; corolla ovoid or ovoid-conical, ca. 1 cm long; stamens 30–50, the filaments linear, flattened, unequal, 3–8 mm long in bud, the anthers linear-oblong, to ca. 5 mm long in bud, sagittate-cordate basally; ovary cylindrical-ovate, abruptly narrowed toward the short style, including the style ca. 6 mm long, 6–8-loculed. *Fruit* globose, ca. 1 cm in diameter, apiculate.

Known from Panama, Colombia, Ecuador, and Peru; vine in rainforests, alt. to 600 m.

DARIEN: Río Areti, *Duke & Nickerson 14919* (MO). Río Balsa, between Manene and Tusijuanda, *Duke 13545* (MO, U). Trail between Río Escucha Ruido and Río Tuira, *Stern et al. 572* (MO).

3. **Marcgravia brownei** (Tr. & Planch.) Krug & Urban, Symb. Ant. 1: 367. 1899.

M. rectiflora var. *brownei* Tr. & Planch., Ann. Sci. Nat. Bot., Sér. 4. 17: 365. 1862.
M. ampulligera Woodson, Ann. Missouri Bot. Gard. 27: 319. 1940.

Large epiphytic *vine* or liana; flowering branchlets pendulous, quadrangular to subterete, lenticellate. *Leaves* subsessile or short-petiolate, the petiole 1–5 mm long and 2–3 mm wide, flattened above; blade oblong, ca. 2.5–3 times as long as wide, 7–14 cm long and (2.5–)3–4.5(–5.5) cm wide, acuminate apically, the acumen 1–2 cm long, acute or attenuate to subrounded and asymmetric basally, coriaceous or thinly coriaceous, the midrib sulcate above, prominent beneath, the lateral veins mostly obscure or obsolete; hypophyllous glands numerous, mostly conspicuous, some large or small glands in an oblique row in the basal part of the blade and a row of small or minute glands ca. 1–4 mm from the margin. *Inflorescences* umbelliform, with 15–30 fertile flowers and ca. 4–5 nectaries; nectaries flask- or pitcher-shaped, stalked, 3–5 cm long, the stalk mostly short, ca. 2–5 mm long (rarely longer), canaliculate, the cup clavate,

2–4 cm long, the neck ca. 3–5 mm in diameter, the inflated part ca. 5–8 mm in diameter, the orifice rounded with a recurved apiculate rim. *Flowers* mostly slightly oblique on the pedicels, the pedicels 3.5–5.5 cm long, stout, lenticellate; bracteoles triangular-ovate to ovate-suborbicular, ca. 2–3 mm long and ca. 2 mm wide; sepals broadly suborbicular, to ca. 5 mm long and to ca. 8 mm wide; corolla conical-ovate, ca. 1.5 cm long, ca. 7 mm in diameter basally; stamens 18–35, the filaments flattened, filiform, 4–10 mm long, the anthers linear, 4–7 mm long; ovary subglobose, abruptly narrowed to the 2–4 mm long style, including the style 5–10 mm long and ca. 4 mm in diameter, 6–9-loculed. *Fruit* globose, apiculate, 1–2 cm in diameter.

Known from Jamaica, Honduras, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, and Bolivia; in montane rainforests and cloud forests, alt. 1000–2500 m.

CHIRIQUI: Vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m, *Woodson & Schery* 577 (GH, MO, US). Boquete district, Bajo Chorro, rainforest, alt. 6000 ft, *Davidson* 398 (F); Cerro Horqueta, dense woodland in cloud forest, alt. 5000 6000 ft, *Duyer & Hayden* 7743 (MO). Humid forest around Los Siguas Camp, S slope of Cerro de la Horqueta, alt. 1700 m, *Pittier* 3195 (US). Trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt. 1500 2000 m, *Allen* 1488 (F, NY, US). Río Chiriquí Viejo valley, *G. White* 90 (F, GH, MO), near El Volcán, *P. White* 186 (F, MO). COCLE: Foothills of Cerro Pilon, near El Valle, alt. ca. 900 m, *Duke & Correa* 14688 (MO, U). El Valle, cloud forest, alt. 800 1000 m, *Duke* 13164 (MO, U).

4. **Maregravia schippii** Standley, Publ. Carnegie Inst. Wash. 461: 71. 1935.—FIG. 6.

Large *vine,* the branchlets mostly angular, with rows of lenticels. *Leaves* subsessile, the petiole 1–2 mm long and ca. 2 mm wide; blade oblong, 2.5–3.5 times as long as wide, 7–12 cm wide, shortly acuminate or acute-subacuminate apically, asymmetric and mostly rounded or obtuse or sometimes acute basally (the first leaf below the inflorescence dimorphic, smaller and relatively wide), coriaceous, the midrib slightly sulcate above, prominent beneath, the lateral veins obscure or obsolete; hypophyllous glands numerous, mostly 2–3 small poriform glands in an oblique row in the basal part of the blade and a row of numerous minute poriform or solid glands within 1 mm from the margin. *Inflorescences* with ca. 7–12 *flowers* and mostly one nectary or none; nectaries flask- or pitcher-shaped, ca. 3.5–4.5 cm long, the stalk 0.5–1 cm long, the cup clavate, 2.5–4 cm long, the orifice with a recurved apiculate rim. *Flowers* erect or slightly oblique on the pedicels, the pedicels 4–6 cm long, lenticellate, especially when fruiting; bracteoles suborbicular to broadly semiorbicular, 1.5–3 mm long and 2–4 mm wide; sepals broadly suborbicular, 4–6 mm long and 6–8(–9) mm wide, the margin without glands; corolla ca. 13 mm long and ca. 7 mm in diameter; stamens ca. 20–30, the filaments linear, flattened, ca. 5 mm long in bud, the anthers linear, ca. 4–5 mm long, sagittate basally; ovary cylindrical-subglobose, abruptly narrowed to the ca. 2 mm long style, including the style ca. 5–8 mm long, ca. 3–4 mm in diameter in bud, 8–9-loculed. *Fruit* unknown.

Rainforests of Atlantic Central America from British Honduras to Panama. Low altitudes, to ca. 1000 m.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, Water Valley, *von Wedel 1763* (GH, MO, US).

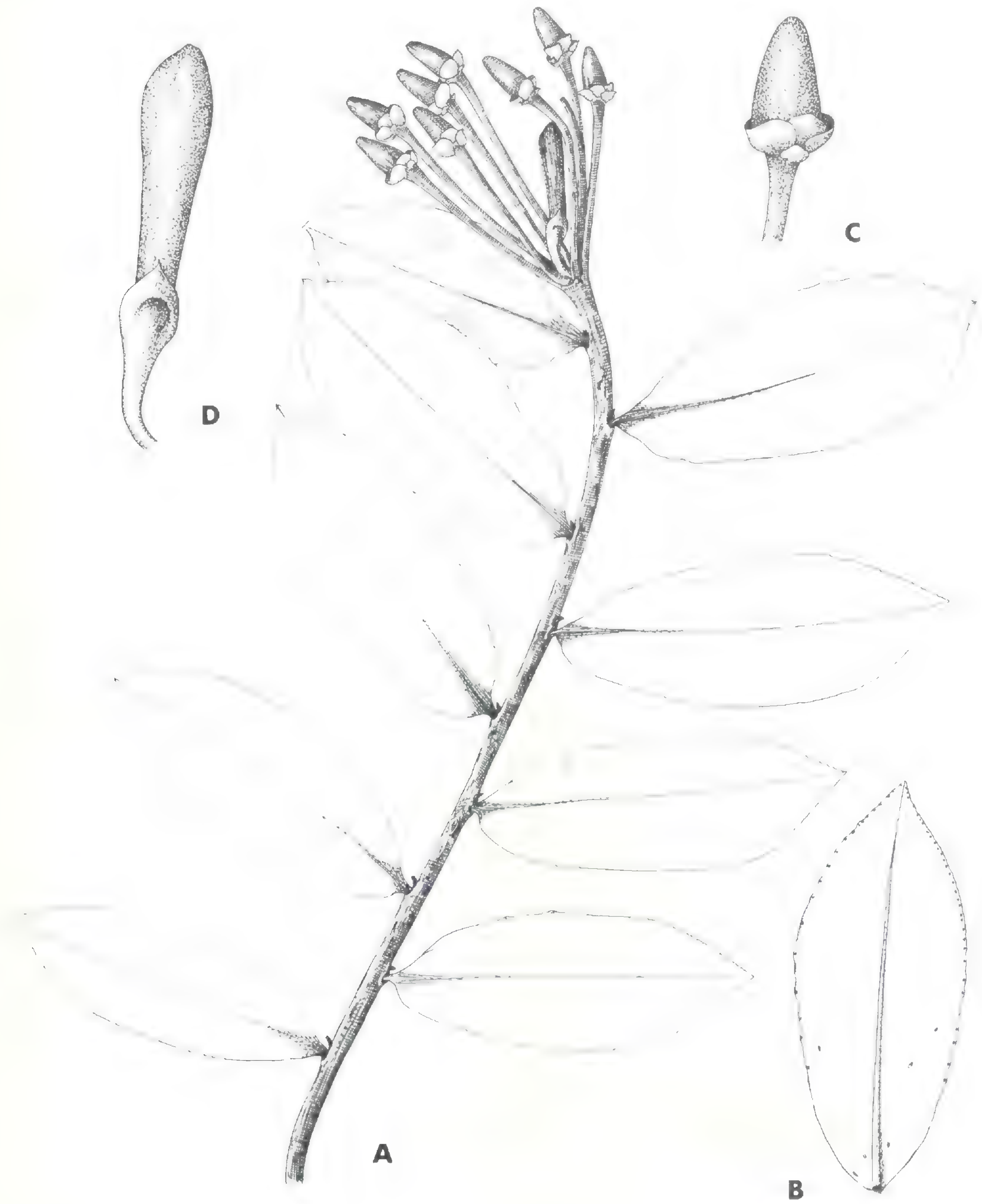

FIGURE 6. *Marcgravia schippii* Standley.—A. Habit (× 3/5).—B. Leaf, abaxial view (× 3/5).—C. Flower (× 1 1/5).—D. Nectary (× 1 1/5). [After *von Wedel 1763* (GH).]

5. **Marcgravia affinis** Hemsley, Diag. Pl. Nov. 1: 3. 1878.

Epiphytic climbing *shrub,* the flowering branchlets slender, lenticellate. *Leaves* subsessile, the petiole 1–2 mm long; blade elliptic, ovate-elliptic, elliptic-oblong, or oblong, 3–9 cm long and 1.5–3.5 cm wide, long-acuminate apically, the acumen 1–1.5 cm long, subacute to rounded basally, chartaceous, mostly remaining green when dried, the midrib, the lateral veins, and the veinlets prominent on both sides of the blade; hypophyllous glands varying, ca. 4 small poriform glands in an oblique row in the basal half of the blade, few dark glands in the revolute margin and numerous minute dark punctiform scattered glands which are often hardly visible with the unaided eye. *Inflorescences* umbelliform, with 6–12(–15) fertile flowers and 2–5 nectaries, the rachis ca. 3 mm long; nectaries cup-shaped, long-stalked, the stalk slender, ca. 10–15 mm long, the cup slightly curved, cylindrical or slightly inflated, ca. 5–12 mm long and 2–4 mm in diameter, the large opening with a revolute rim. *Flowers* oblique on the pedicels, the pedicels 2–3 cm long and to 1 mm in diameter, lenticellate; bracteoles semi- to suborbicular, 1–2(–3) mm wide and 0.5–1(–2) mm long; sepals broadly semi- to suborbicular, 2–4 mm wide and 1–3 mm long; corolla ovate-conical, ca. 6 mm long, ca. 3–4 mm in diameter; stamens 12–20, the filaments flattened, ca. 3 mm long in bud, the anthers ca. 2–2.5 mm long, sagittate-cordate basally; ovary subglobose, ca. 2 mm in diameter, ca. 2 mm long, sulcate, ca. 6–7-loculed, the style ca. 1.5 mm long. *Fruit* globose, ca. 6–7 mm in diameter, apiculate.

Known from Costa Rica, Panama, and Colombia. Epiphytic climber in cloud forests.

BOCAS DEL TORO: Between Criollo (just above Buena Vista) and Quebrada Higueron, cloud forest, *Kirkbride & Duke 771A* (MO). DARIEN: Cerro Pirre, *Bristan 616* (U); cloud forest, *Duke 6120* (MO); west slope, *Duke 6594* (MO).

6. **Marcgravia membranacea** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 697. 1937.—Fig. 7.

Woody *vine,* the flowering branchlets slender, somewhat angular, lenticellate, mostly flexuous, ending in a slender peduncle. *Leaves* large, the petiole 3–8 mm long, canaliculate above; blade oblong or elliptic-oblong, 2–3 times as long as wide, 12–21 cm long and 5–9 cm wide, acuminate apically, the acumen 1–1.5 cm long, obtuse or subrounded basally, chartaceous and remaining greenish when dried, the midrib slightly sulcate and often prominent above, prominent beneath, the main lateral veins in ca. 7–8 pairs, slightly prominent above, strongly prominent beneath, the veinlets conspicuous, especially beneath; hypophyllous glands small, 2 at the base near the midrib and some inconspicuous poriform glands with a circumvallation in a row ca. 2–5 mm from the margin, dark glands in the margin; leaves subtending the peduncle much smaller and mostly shed early. *Inflorescences* pendulous, the peduncle slender, 15–30 cm long, with ca. 10–16 fertile flowers and ca. 5 nectaries; nectaries urceolate, sessile or subsessile, ca. 15 mm long, the opening narrow with a funnel-shaped rim. *Flowers* oblique on the pedicels, the pedicels ca. 1.5 cm long, lenticellate, often hirtel-

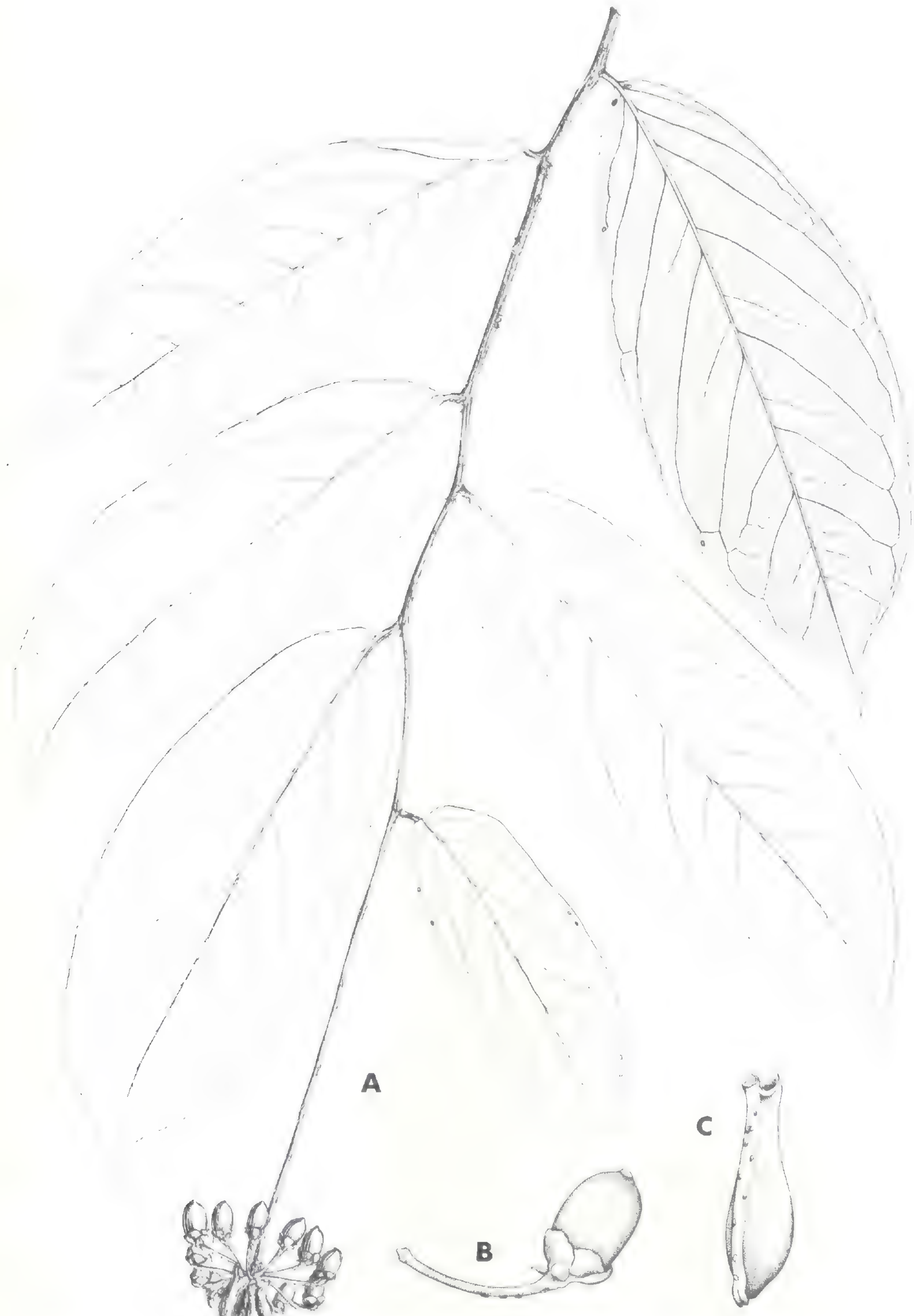

FIGURE 7. *Marcgravia membranacea* Standley.—A. Habit (× ½).—B. Flower (× 1½).—C. Nectary (× 2). [A, after *Allen 1739* (US) and *Standley & Valerio 47089*, Costa Rica (F); B–C, after *Standly & Valerio 47089*, Costa Rica (F).]

lous, rough, especially in fruit, often somewhat reflexed; bracteoles ovate-suborbicular, often slightly puberulent, 2–3 mm long and 2–3 mm wide; sepals broadly suborbicular, ca. 3–4 mm long and ca. 5–6 mm wide, the margin glandular, often puberulent; corolla ovate-subglobose, to ca. 10 mm long and ca. 6 mm in diameter, the apex apiculate; stamens ca. 30–35, the filaments flattened, ca. 5 mm long in bud, the anthers 2–3 mm long in bud; ovary subglobose, densely puberulent, ca. 3–5 mm in diameter, with the style 4–6 mm long, 9–10-loculed. *Fruit* unknown.

Known from Costa Rica and Panama.

COCLE: North rim of El Valle de Antón, alt. 600–1000 m, *Allen 1739* (F, GH, US); La Mesa, above El Valle, cloud Forest, alt. 600–800 m, *Duke & Dwyer 15160* (U).

7. **Maregravia atropunctata** de Roon, Acta Bot. Neerl. 18: 197. *pl.* 2. 1969.

Epiphytic climbing *shrub*, the flowering branchlets quadrangular, with rows of lenticels. *Leaves* large, the petioles 5–10 mm long and 2–3 mm wide, canaliculate above; blade elliptic-oblong, 12–18 cm long and 6–9.5 cm wide, acuminate apically, the acumen 0.5–1 cm long, obtuse or rounded basally, rigidly coriaceous, the midrib stout, as the lateral veins prominent on both sides of the blade; hypophyllous glands minute, dark, punctiform, numerous, regularly scattered. *Inflorescences* umbelliform, few-flowered; nectaries unknown. *Flowers* erect on the pedicels, the pedicels ca. 1.5 cm long, lenticellate; bracteoles ca. 3 mm wide; sepals suborbicular or broadly suborbicular, ca. 5 mm wide; corolla and stamens unknown; ovary ca. 7-loculed. *Fruit* unknown.

Known from the type locality only.

COCLE: Cerro Caracoral, elfin forest, alt. ca. 1000 m, *Duke & Dwyer 15116* (U).

Though the single available specimen is incomplete, the species is easily recognized and cannot be confused with any other species of the genus.

8. **Maregravia nepenthoides** Seemann, Jour. Bot. 8: 245. 1870.—Fig. 8.

M. tonduzii Gilg, Bot. Jahrb. Syst. 42: 125. 1908.

Large woody *vine*, the branchlets angular, with rows of lenticels, often flexuous. *Leaves* large, the petioles 3–9 mm long, canaliculate above; blade oblong, 2.5–3.5 times as long as wide, 10–20(–25) cm long and 3–6(–7.5) cm wide, acuminate apically, the acumen 1–1.5 cm long, obtuse to rounded or sometimes subacute basally, coriaceous or subcoriaceous, rarely chartaceous, the midrib sulcate above, prominent beneath, the major lateral veins in ca. 10 pairs, alternating with minor ones, forming a marginal vein, prominent on both sides of the blade, the veinlets prominent at least beneath; hypophyllous glands small, mostly inconspicuous and hardly visible with the unaided eye, in a row of 6–15, 1–8 mm from the margin, minute dark glands in the margin. *Inflorescences* umbelliform, with 20–35 or possibly more fertile flowers and 5–6 nectaries, the rachis globose, 6–9 mm in diameter; nectaries large, dipper-shaped, 5–7.5 cm long, the stalk 3–4 cm long, canaliculate inside, lenticellate outside, the cup 1.5–3.5 cm long and 1–2 cm wide, the opening large. *Flowers* perpendicular on the

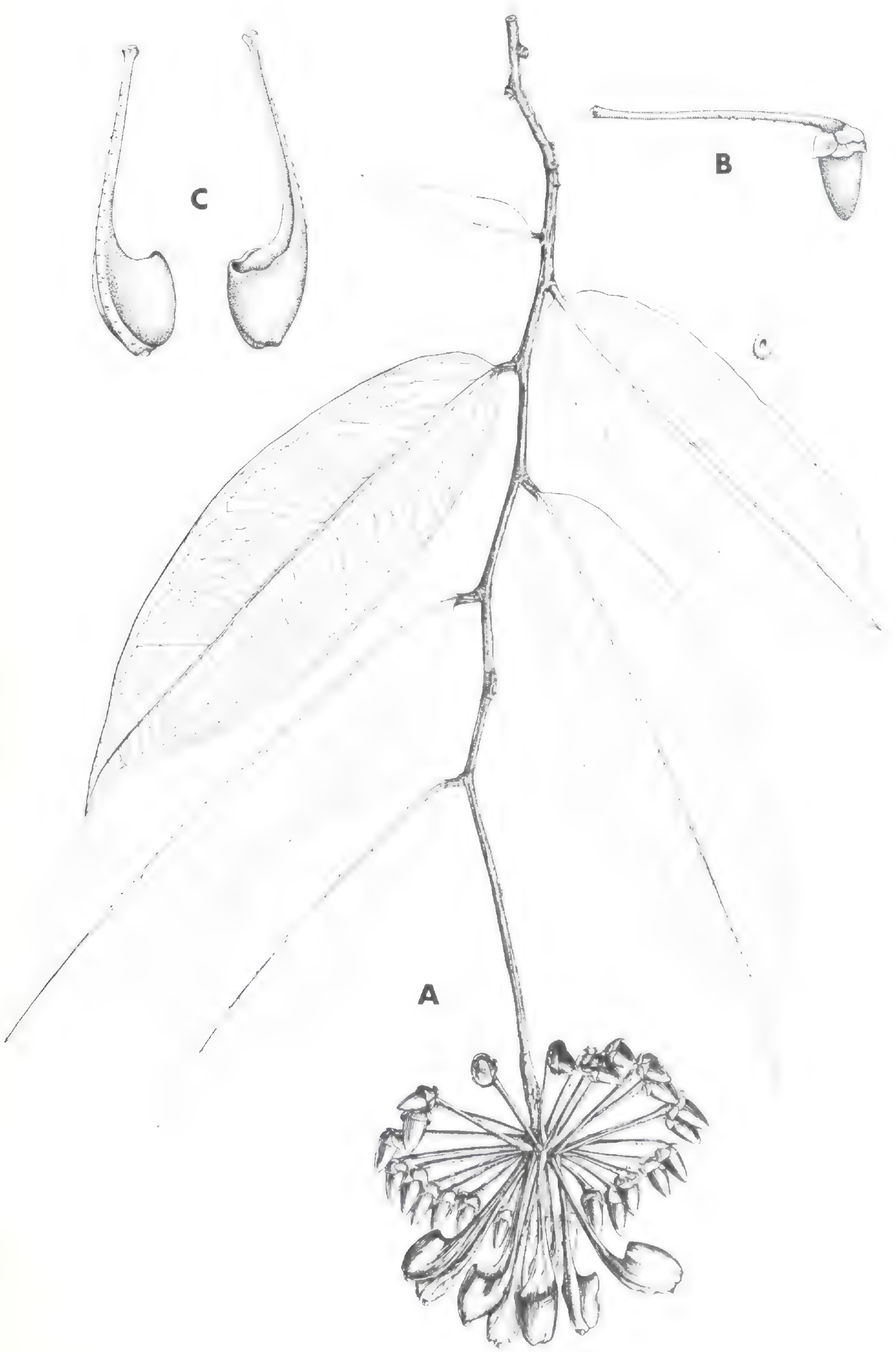

FIGURE 8. *Marcgravia nepenthoides* Seemann.—A. Habit (× ½).—B. Flower (× 1).—C. Nectaries (× ¾). [After *Wetmore & Abbe* 95 (F).]

pedicels, the pedicels 2–3.5 cm long, to 4.5 cm long in fruit, lenticellate; bracteoles broadly suborbicular, 2–3.5 mm long and 3–5 mm wide; sepals unequal, suborbicular or semiorbicular, 3–4 mm long and 5–6.5 mm wide; corolla conical, 8–10 mm long and 4–5 mm in diameter basally; stamens ca. 25–30, the filaments linear, flattened, 3–8 mm long, the anthers ca. 2 mm long; ovary subglobose, ca. 3 mm in diameter, with a short style, ca. 10-loculed. *Fruit* globose, apiculate.

In tropical rainforests of the Atlantic region of Central America from British Honduras to Panama.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1192* (GH, US); Water Valley, *von Wedel 818* (GH, US), *1666* (MO). CANAL ZONE: Barro Colorado Island, *Aviles 67* (F); near dock, *Shattuck 666* (F); near boat landing, *Wetmore & Abbe 95* (F, GH).

It was on this species that Thomas Belt made his remarkable observations about pollination by birds through which the genus *Marcgravia* became a classic case of ornithogamy. Since then it has become known that only some species of *Marcgravia* are pollinated by birds and others by bats.

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 152. PRIMULACEAE[1]

SUSAN VERHOEK-WILLIAMS[2]

Annual or perennial *herbs*, rarely shrubs. *Leaves* alternate, opposite, or verticellate, sometimes all basal, usually simple, exstipulate. *Inflorescences* umbellate or single-flowered at the end of a scape, or in terminal or axillary racemes, spikes, or panicles, or flowers solitary and axillary. *Flowers* (4–)5(–9)-merous, bisexual, usually regular; calyx gamosepalous, often deeply lobed, persistent; corolla absent, polypetalous, or gamopetalous, often deeply lobed, rotate, salverform, or with the lobes reflexed; stamens as many as and opposite the corolla lobes or petals, occasionally accompanied by antisepalous staminodia, the anthers 2-loculed, introrse, dorsifixed or basifixed, longitudinally dehiscent or rarely with terminal pores; gynoecium 5-carpellate, the ovary superior or half inferior, unilocular, the placentation free-central, the style 1, often heterostylous, the stigma 1, capitate; ovules few to many. *Fruit* capsular; seed with straight embryo and abundant, hard to firm, semitransparent endosperm.

A family of about 22 genera and nearly 1000 species, widely distributed but primarily of temperate regions, especially in the mountainous parts of the northern hemisphere. Only the genus *Anagallis* is known from Panama.

1. ANAGALLIS

Anagallis L., Sp. Pl. 148. 1753.

Annual or perennial *herbs*, erect, decumbent, or prostrate, glabrous, the stem terete, winged or angled. *Leaves* opposite, alternate, or verticillate, sessile or short-petiolate, entire. *Inflorscences* terminal racemes or flowers solitary and axillary. *Flowers* regular, (4–)5–6(or rarely –9)-merous, sessile or pedicellate, red, pink, blue, or white; calyx deeply lobed, the lobes ± lanceolate; corolla usually equaling or exceeding the calyx, gamopetalous, rotate or rotate-campanulate, sometimes marcescent, deeply lobed, the lobes sometimes gland fringed, the tube short, the stamens inserted on the base of the corolla tube and partially adnate to it, the filaments connate basally, glabrous or bearded, the anthers ovoid, longitudinally dehiscent; staminodia absent; ovary superior, globose, the style filiform. *Fruit* an indehiscent capsule or a pyxis, globose; seeds small, numerous and angular, or rarely 1 and globose.

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[1]Assisted by National Science Foundation Grant GB-5674.
[2]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 57: 51 54. 1970.

A genus of 29 species growing in damp places from sea level to 12,000 ft; mostly native to Africa, the Mediterranean region, and South America but with two native and one introduced species widespread in both hemispheres. One species is reported from Panama.

Pax and Knuth in their monograph of the Primulaceae (Pflanzenr. IV. 237: 1–386. 1905) separated *Centunculus minimus* L. from *Anagallis* as a monotypic genus. This treatment has been followed by some later authors, but recently P. Taylor (Kew Bull. 10: 321–350. 1955) has included *Centunculus* with some related species of *Anagallis* as a subgenus of *Anagallis* on the basis that the characters of corolla length and filament adnation which have been used to separate the two genera form a continuum. I find no compelling reasons to maintain the division at the generic level and have written the generic description to include *Anagallis* (*Centunculus*) *minimus*.

1. **Anagallis pumila** Sw. var. **pumila**, Prod. Veg. Ind. Occ. 1: 40. 1788.—FIG. 1.

Centunculus pentandrus R. Br., Prodr. 427. 1810.

Slender, annual *herbs*, simple or branched, erect or sometimes trailing, the stems slightly angled, to 30 cm long. *Leaves* mostly alternate, sometimes opposite basally, sessile, the lower sometimes suborbicular, the upper ovate to ovate-elliptic, mucronulate apically, gland-dotted, 5–8 mm long and 2–4 mm wide. *Flowers* solitary, axillary, white; pedicels 3–6 mm long, usually equaling or exceeding the leaves; calyx lobes lanceolate, faintly 3-nerved, gland-dotted, 2–3 mm long and less than 1 mm wide; corolla rotate, often marcescent at the top of the capsule, the lobes ovate-lanceolate, 2–3 mm long, usually equaling the calyx; filaments glabrous, adnate only near the base of the corolla, less than 1 mm long, the anthers basifixed. *Fruit* a pyxis, ca. 1.5 mm in diameter; seeds numerous, triangular-ellipsoid, black, the coat tubercular.

A cosmopolitan variety native to Florida, from Mexico through Central America and the West Indies into tropical South America, and in southern Asia, Africa, and Australia.

CHIRIQUI: Boquete, swamp, *Davidson* 579 (F, MO); alt. 1200 1500 m, *Woodson & Schery* 799 (MO). COCLE: Penonomé & vicinity, alt. 50–1000 ft, *Williams* 203 (NY, US). Between Puerto Posado & Penonomé, *Williams* 162 (NY). PANAMA: Las Sabanas, swamp, *Bro. Heriberto* 149 (US). Near Matías Hernández, *Standley* 29000 (US). Between Matías Hernandez and Juan Díaz, *Standley* 31986 (US). Nuevo San Francisco, *Standley* 30772 (US). Along road between Panamá & Chepo, savannas, *Dodge et al.* 16662 (MO). Vicinity of Juan Franco Race Track, near Panamá, *Standley* 27825 (US). Near big swamp E of Río Tocumen, *Standley* 26625, 26708 (both US).

The other variety of this species, var. *barbata* P. Taylor (Kew Bull. 10: 345. 1955), is native to the highlands of Africa. It is distinguished from var. *pumila* by bearded filaments and corolla lobes which are 2.5–4 mm long.

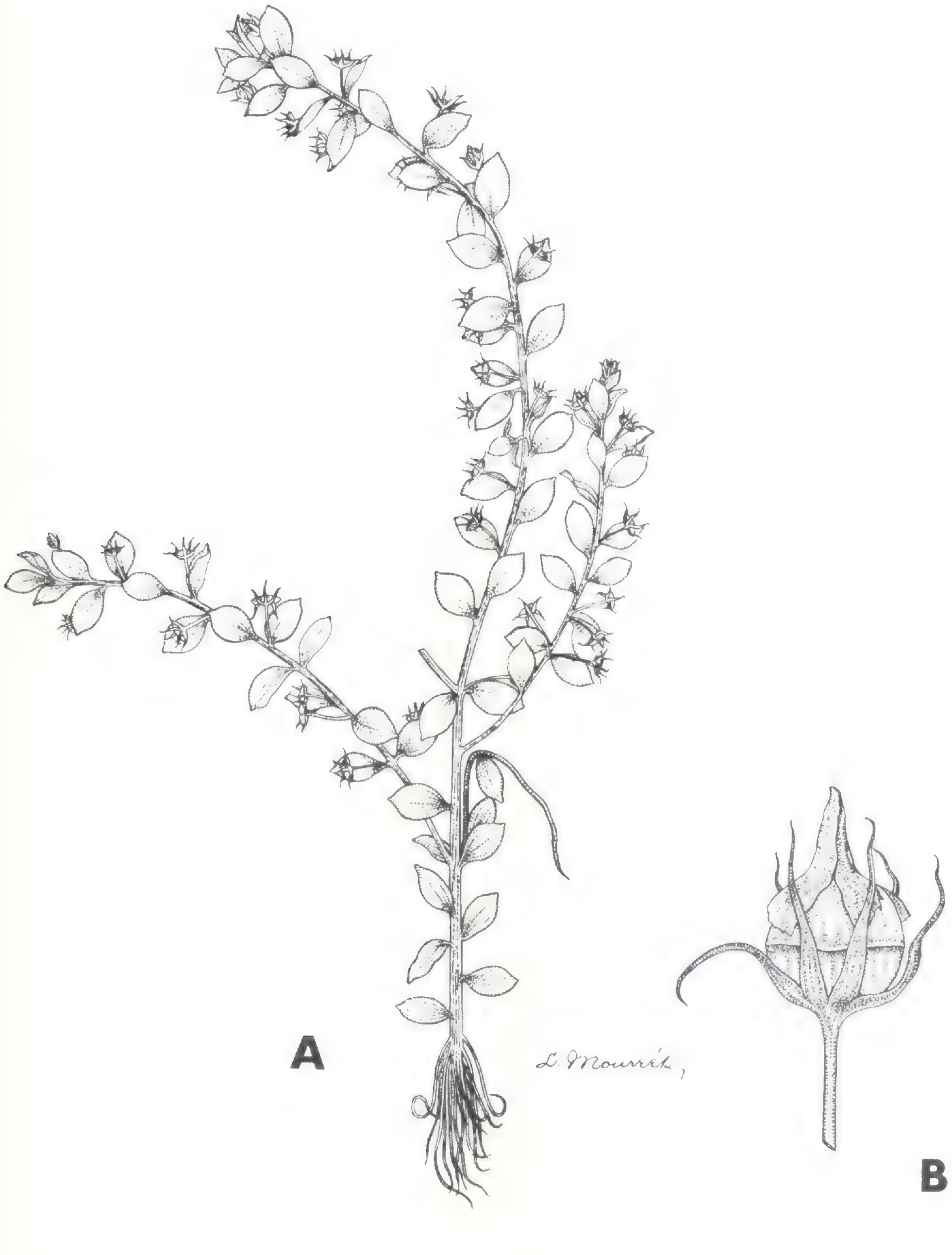

FIGURE 1. *Anagallis pumila* Sw. var. *pumila*.—A. Habit (× 2).—B. Pyxis (× 13). [A, after *Bro. Heriberto 149* (US); B, after *Davidson 579* (MO).]

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Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

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—var. pumila **52**
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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 153. PLUMBAGINACEAE[1]

SUSAN VERHOEK-WILLIAMS[2]

Herbs or subshrubs, perennial, rarely annual, sometimes scandent, the branches with chalk glands. *Leaves* alternate or rosulate, simple, entire, with mucilage or chalk glands, exstipulate. *Inflorescences* various, racemose, cymose, or paniculate. *Flowers* bisexual, regular, 5-merous; calyx gamosepalous, with stalked mucilage glands or eglandular, the tube 5–10 ribbed, the lobes scarious and showy, or membranous, persistent; corolla sympetalous or petals nearly separate, the lobes imbricate in bud; stamens 5, opposite the corolla lobes, hypogynous or epipetalous, the anthers 2-loculed, introrse, longitudinally dehiscent; ovary superior; 5-carpellate, unilocular, styles 5, often heterostylous, free or connate basally, the stigmas linear or capitate; ovule 1, pendulous from a basal funicle. *Fruit* an achene, utricle, or capsule, wholly or partly included in the calyx; seed with straight embryo and crystalline-granular endosperm.

A cosmopolitan but primarily Old World family of 10 genera and about 325 species, mostly of semi-arid situations, on saline and calcareous soils. Only *Plumbago* is reported from Panama.

The Plumbaginaceae are of slight economic importance. A few are cultivated as ornamentals, and some species of *Plumbago* are used medicinally as a source of plumbagin, a vesicant quinone employed as a counter-irritant and vermifuge in this hemisphere, for relief from toothache in France, and in India as a remedy for ailments from dyspepsia to leprosy and plague. Plumbagin affects the mucous membranes, produces blisters very readily, and can be poisonous when taken internally (*cf.* R. H. Thomson. 1957. Naturally Occurring Quinones. New York).

1. PLUMBAGO

Plumbago L., Sp. Pl. 151. 1753.

Herbs or subshrubs, perennial, the stems often scandent or reclining; branches striate, glabrous, sparsely dotted with chalk glands. *Leaves* alternate, dotted with chalk-secreting glands, sessile and auriculate-amplexicaul, or petiolate, the petiole amplexicaul and sometimes auricled basally, paler below and lepidote-appearing from chalk secretions. *Inflorescences* racemose or basally paniculate and gradually becoming racemose toward the apex, the axis with mucilage glands or eglandular, pubescent or glabrous. *Flowers* pedicellate, each subtended by a bract

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[1]Assisted by National Science Foundation Grant GB-5674.

[2]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

and 2 bracteoles, the bract with chalk glands; calyx tubular, the lobes erect, membranous between the ribs, the ribs bearing stalked mucilage glands; corolla salverform, the tube slender, long exserted; stamens hypogynous, only slightly exserted, the filaments dilated basally, the anthers linear; styles filiform, usually homostylous, partly connate basally, stigmatic along their inner surfaces. *Fruit* an achene, utricle, or capsule, membranous, indehiscent or dehiscent circumcissally or into 5 sometimes apically connate valves, included in the calyx; in Panama the fruit a capsule, the valves separating first near the middle.

A genus of *ca.* 20 species in the tropics and subtropics, occasionally reaching into temperate areas. Two species occur in Panama, one native and one an escape from cultivation.

a. Calyx puberulent, the ribs bearing stalked glands only on the distal portion; petioles auriculate; inflorescence short and dense, the rachis pubescent, eglandular . . . . . 1. *P. auriculata*

aa. Calyx glabrous, the ribs bearing stalked glands along the entire length; petioles not auriculate; inflorescence elongate, the rachis glabrous, usually bearing mucilage glands . . . . . 2. *P. scandens*

1. **Plumbago auriculata** Lam., Encycl. 2: 270. 1786.—Fig. 1.

Plumbago capensis Thunb., Prod. Pl. Cap. 1: 33. 1794.

Subshrubs to 2 m, sub-scandent. *Leaves* ovate-elliptic to spatulate, narrowed to the obtuse apex, gradually attentuate basally into a short petiole, 3–6(–9) cm long and 1–2(–3) cm wide, glabrous, copiously calciferous-glandular below, the petioles auriculate basally, the auricles adnate to the stem, reniform or occasionally as long as wide, 3–6 mm wide and 2–3 mm long; the main stem leaves commonly with smaller leaves fasciculate in the axils. *Inflorescences* densely-flowered racemes, 2–6 cm long, the rachis pubescent, the bracts and bracteoles puberulent, the bracts lanceolate, 5–7(–9) mm long. *Flowers* with pedicels ca. 1 mm long; calyx 1–1.3 cm long and 1–2 mm wide, puberulent, the teeth triangular, ca. 1 mm long, the ribs with stalked glands along the distal ½ to ⅔; corolla showy, usually azure, occasionally white, the tube 2.7–4 cm long, the limb 2–2.5(–2.9) cm in diameter, the lobes broadly spatulate. *Capsules* slenderly elongate-ovoid, pentagonal, ca. 8 mm long, the apex obtuse; seed nearly filling the capsule, slightly 5-angled, grooved along one side, the funicular end acute and distinctly 5-angled, the base truncate, 6–7 mm long, black.

Native to South Africa, but widely cultivated, and naturalized in warmer regions; in our hemisphere occurring outside of cultivation at least in Florida, Mexico, Guatemala, Panama, Venezuela, and Paraguay.

VERAGUAS: Cañazas, *Tyson 3649* (MO).

This species has long been recognized and cultivated under the name *Plumbago capensis* Thunb. However, after examining the type of *Plumbago auriculata* Lam., C. E. Wood, Jr. (Baileya 16: 137. 1968) has determined that *P. auriculata* is the correct name for the species.

Due to the paucity of Panamanian material, the above description, with the exception of fruit and seed, is also based on Mexican and Central American

material. The fruit and seed description are from an African collection [SOUTH AFRICA: Uitenhaag District, *Ecklon & Zeyher s.n.* (MO)]. Except that the African and some of the Mexican specimens tend to be more woody, there is ample correspondence between them and the Panamanian specimen.

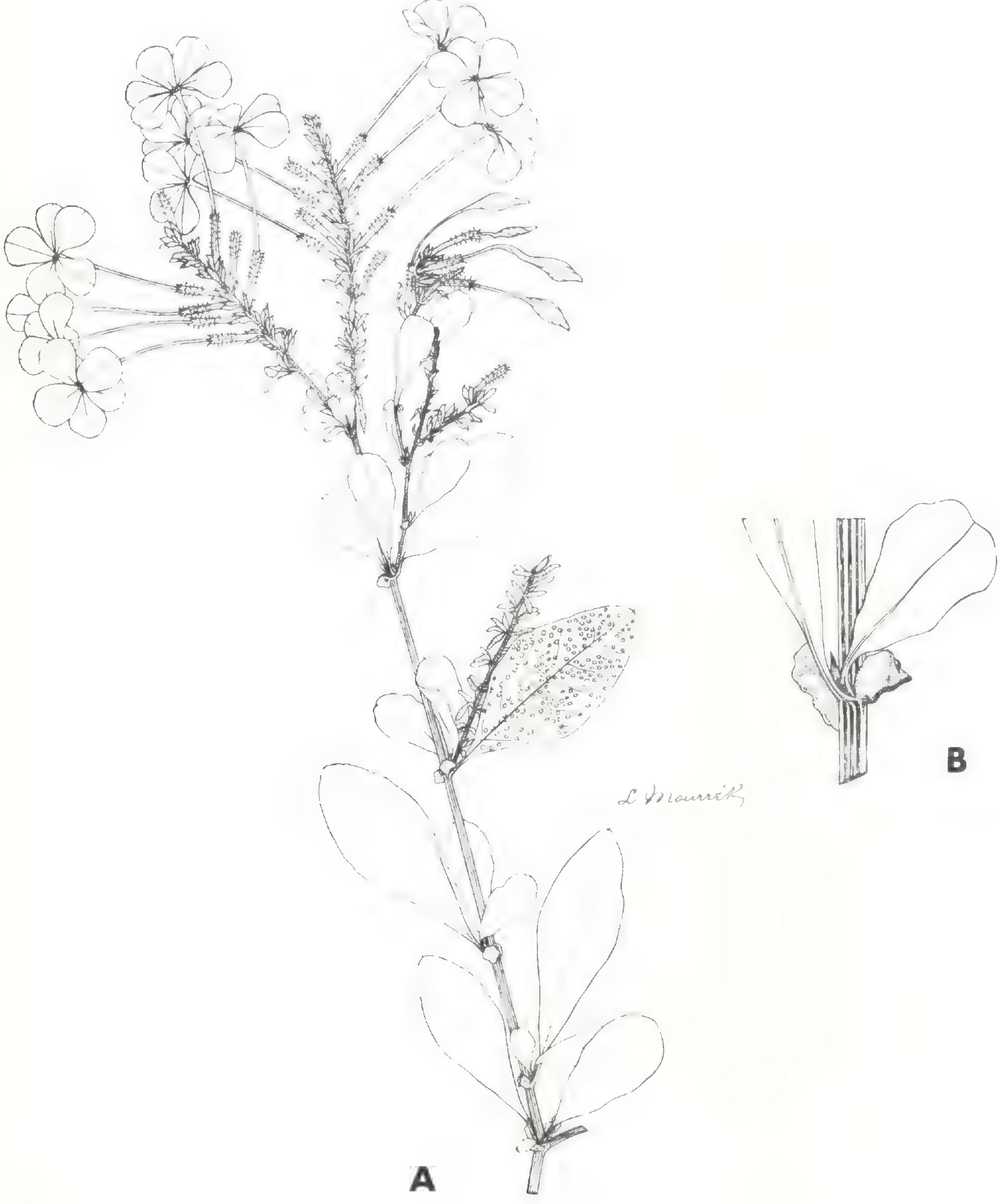

FIGURE 1. *Plumbago auriculata* Lam.—A. Habit (× ¼).—B. Petiole base showing auricles and attachment to stem (× 6). [After *Tyson* 3649 (MO).]

2. **Plumbago scandens** L., Sp. Pl. ed. 2. 215. 1762.

Scandent, suffrutescent plants, erect to ca. 1 m or straggling to 2 m. *Leaves* ovate-lanceolate, acute to acuminate apically, acute and petiolate basally, 5–9 cm long and 2–4 cm wide, glabrous, the petioles 5–10 mm long, amplexicaul. *Inflorescences* branched basally, the main axes forming elongate, slender racemes 10–12 cm long, the rachis glabrous, bearing nearly sessile mucilage glands, the bracts and bracteoles glabrous, sometimes with sessile mucilage glands, the bracts lanceolate, long-acuminate, ca. 4 mm long. *Flowers* with pedicels to 1 mm long, calyx 8–10 mm long and ca. 2 mm wide, glabrous, the teeth cuspidate-uncinate, ca. 1 mm long, the ribs with stalked glands along the entire length; corolla white, the tube 1.5–2 cm long, the lobes of the limb obovate-mucronate, 6–8 mm long. *Capsules* elongate-ovoid, slightly pentagonal, ca. 7 mm long, elongate-conical apically; seed somewhat flattened, inequilaterally ovoid, grooved along one side, gradually attenuate to the funicular end, slightly 5-angled apically, truncate basally, ca. 6 mm long.

Southern Florida, Texas, and Arizona; Mexico, Central America, the West Indies, and South America.

CANAL ZONE: Corozal to Pedro Miguel, *Cowell 410* (NY). COCLE: Between Aguadulce and Río Chico, savannas & thickets, alt. ca. 20 m, *Pittier 5005* (US). HERRERA: Road from La Avena to outskirts of Pesé, alt. ca. 200 ft, *Burch et al. 1277* (COL, F, GH, MO, NY, SCZ, UC, US). PANAMA: Near beach at Nueva Gorgona, *Duke 4498* (MO). PROVINCE UNKNOWN: Without locality, *Halsted,* 1850 (NY); *Seeman s. n.* (GH).

Kuntze (Rev. Gen. Pl. 2: 396. 1891) recognized a densely flowered variety, *P. scandens* var. *densiflora,* from St. Thomas, Virgin Islands, differentiating it from the typical variety with its long, lax, more or less interrupted inflorescences. If varieties are to be recognized at all, the Panamanian material is best referred to the typical variety.

Plumbago scandens is closely related to the Old World species *Plumbago zeylanica* L., and the two are perhaps conspecific. Tradition seems to be the main factor in their separation. Consistent characters differentiating the two are lacking, especially where African populations of *P. zeylanica* are involved.

INDEX OF LATIN NAMES

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 162. APOCYNACEAE[1]

JOAN W. NOWICKE[2]

Trees, shrubs, lianas, or herbs, annual or perennial, chiefly lacticiferous. *Leaves* mostly opposite, sometimes alternate, spiral, ternate, or quadrate, simple, entire, glandular at the base of the midrib or non-glandular, occasionally with glands along the entire midrib, the blade pinnately-nerved; stipulate or estipulate, mostly petiolate, sometimes perfoliate and forming stipular-like rings at the nodes, frequently with glands in the axils. *Inflorescences* dichasial cymes or racemes, frequently modified by unequal suppression and reduction of lateral branches. *Flowers* bisexual, mostly regular, bracteate or bracts apparently absent; sepals (4–)5, connate basally, equal to conspicuously unequal, mostly imbricate, the lobes with or without internal basal glands (squamellae); petals (4–)5, connate, mostly salverform or infundibuliform, with or without appendages, the limb (4–)5-lobed, contorted in bud; stamens (4–)5, included or exserted, epipetalous, alternate, the filaments short or absent, the anthers free and not agglutinated to the stigma or connivent and agglutinated to the stigma, with or without an enlarged connective, pollen granular or subglutinous and in tetrads; gynoecium 2(–5–8)-carpellate, apocarpous to syncarpous, the ovary superior, rarely subinferior, 2-locular with axile placentae or 1-locular with parietal placentae, the ovules 1 to many per locule, the style usually 1, the stigma massive and complex, frequently umbraculiform below and capitate or pentagonal above. *Fruit* apocarpous or syncarpous, of 1 or 2 follicles, a berry, a capsule, or ± drupaceous; seeds 1 to many, dry or arillate, naked, pubescent, winged or apically comose.

A family of 200–300 genera and 1300–2000 species in the tropics and subtropics of both hemispheres and occasionally in temperate regions.

Economically, the family is important for its ornamentals: *Vinca* (periwinkle), *Nerium* (oleander), *Ervatamia* (crepe-jasmine), *Plumeria* (frangipani), and *Amsonia*. Many species have toxic alkaloids and glycosides.

Twenty-seven genera are found in Panama. Although I consider most of these taxa to be distinct and readily separable, an artificial key to genera is provided as well as a natural one, since the latter key frequently involves the verification of characters which can be observed only after tedious boiling and careful dissec-

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tion of flowers. However, it must be stressed that both keys are for Panamanian material only, and broader use may lead to misidentification.

One other genus may be present in Panama. *Couma macrocarpa* Barb. Rodr. has been reported from Colón, *Holdridge 6270* (MO), and from an unknown province, *Salas 12500* (F); the latter collection may be erroneously labeled. However, these collections, Panamanian or otherwise, consist of a single leaf and 3 unattached leaves, and I consider positive identification impossible.

Woodson's infrafamilial classification (Ann. Missouri Bot. Gard. 17: 9–10. 1930; N. Amer. Fl. 29: 103–105. 1938) has been followed in the arrangement of the natural key. He divided the Apocynaceae into three subfamilies, the Plumerioideae (as Plumeroideae), the Echitoideae, and the Apocynoideae, based largely on the characteristics of the androecium. The Apocynoideae, a small subfamily not represented in Panama, are similar in anther characters to the Echitoideae and are separated only by the tetradinous pollen and non-glandular calyx of the former. Pichon (Bull. Soc. Bot. France 95: 211–215. 1948) revised the larger taxa within the family, and while his enlargement of the Apocynoideae by the addition of the Echitoideae has some merit, his division of this subfamily appears to be based on a vague and difficult character — the shape of the anther connective.

Useful references:

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_____. An evaluation of the genera *Plumeria* L. and *Himatanthus* Willd. Ann. Missouri Bot. Gard. 25: 189–224. 1938.

Natural Key to Genera

a. Anthers completely fertile, without an enlarged connective, free from each other, not agglutinated to the stigma, the pollen tetrads separating into individual grains; calyx lobes with or without glands (squamellae) basally (Subfam. Plumerioideae).
  b. Ovary apocarpous; fruit apocarpous, with 2 follicles (Tribe Plumerieae).
    c. Ovaries with numerous ovules; fruits with numerous seeds.
      d. Calyx lobes with squamellae basally; seeds arillate.
        e. Calyx lobes and bracts small, not foliaceous, and not imbricate; corolla mostly salverform.

f. Leaves large, at least some 20–30 cm long, the midrib enlarged vertically near the base; "follicles" subglobose . . . 1. *Bonafousia*
ff. Leaves smaller, < 16 cm long, the midrib not conspicuously enlarged vertically near the base; follicles ± reniform, acute or acuminate apically.
g. Corolla tube < 16 mm long; flowers single . . . . . 2. *Tabernaemontana*
gg. Corolla tube > 18 mm long; flowers double or single . . . . . 3. *Ervatamia*
ee. Calyx-lobes and bracts mostly large and foliaceous, imbricate; corolla salverform or infundibuliform . . . . . 4. *Stemmadenia*
dd. Calyx lobes without squamellae; seeds not arillate.
h. Plants woody; ovary without a nectary, or with a single annular or 5-lobed nectary.
i. Ovules multiseriate; flowers large and showy.
j. Bracts minute; calyx regular; seeds with an eccentric basal wing; stems with pronounced leaf scars . . . . . 5. *Plumeria*
jj. Bracts conspicuous; calyx minute or obsolete; seeds with an essentially concentric wing; stems without pronounced leaf scars . . . . . 6. *Himatanthus*
ii. Ovules 2-seriate; flowers small.
k. Trees; leaves alternate; follicles large, woody, conspicuously compressed laterally; seeds with a large concentric wing . . . . . 7. *Aspidosperma*
kk. Shrubs; leaves in whorls of 3 or 4; follicles small, not woody or conspicuously compressed laterally; seeds irregularly ciliate along the margins . . . . . 8. *Tonduzia*
hh. Plants herbaceous; ovary with 2 ovoid nectaries.
l. Corolla salverform; flowers 1–3 in the leaf axils . . . . . 9. *Lochnera*
ll. Corolla infundibuliform; flowers solitary in leaf axils . . . . 10. *Vinca*
cc. Ovaries with 1–6 ovules; fruits 1-seeded by abortion . . . . . 11. *Anechites*
bb. Ovary apocarpous or syncarpous; fruit syncarpous, berry like, drupaceous, or capsular.
m. Ovary apocarpous or syncarpous, 2-loculed, placentation axile (Tribe Rauvolfieae).
n. Flowers large and showy; calyx with squamellae; leaves spiral . . . 12. *Thevetia*
nn. Flowers small; calyx without squamellae; leaves opposite or whorled.
o. Leaves whorled, in groups of 4, sometimes 3, anisophyllous within a whorl . . . . . 13. *Rauvolfia*
oo. Leaves opposite, isophyllous within a pair . . . . . 14. *Lacmellea*
mm. Ovary syncarpous, 1-loculed, placentation parietal (Tribe Arduineae). . . . . 15. *Allamanda*
aa. Anthers completely fertile or partially sterile, the connective enlarged, connivent with each other and agglutinated to the stigma, the pollen grains remaining in tetrads; calyx lobes with glands basally, absent in *Rhabdadenia* (Subfam. Echitoideae).
p. Anthers uniformly fertile, the connective with obtuse basal lobes; leaves glandular on the midrib, at least basally.
q. Inflorescences compound.
r. Corolla infundibuliform; inflorescences branching repeatedly; bracteoles conspicuous . . . . . 16. *Allomarkgrafia*
rr. Corolla salverform; inflorescences obscurely dichotomous, branching 1–2 times; bracteoles minute . . . . . 17. *Mesechites*
qq. Inflorescences simple . . . . . 18. *Mandevilla*
pp. Anthers with conspicuous sterile bases, or if rarely uniformly fertile, then the connective with slender or attenuate basal lobes; leaves non-glandular except in some species of *Forsteronia*.
s. Calyx lobes with squamellae basally.
t. Squamellae alternate with the calyx-lobes or irregularly distributed.
u. Corolla salverform and small.
v. Inflorescences thyrsiform or spicate; seeds comose apically . . . . . 19. *Forsteronia*

vv. Inflorescences umbellate; seeds uniformly pubescent . . . 20. *Malouetia*
uu. Corolla infundibuliform, large and conspicuous.
w. Corolla with appendages within; leaves ternate . . . . . 21. *Nerium*
ww. Corolla without appendages; leaves opposite.
x. Leaves peltate . . . . . 22. *Peltastes*
xx. Leaves not peltate, obtuse basally . . . . . 23. *Odontadenia*
tt. Squamellae as many as the calyx-lobes and opposite them, sometimes lacerate.
y. Corolla not appendaged within and without a callous orifice.
z. Corolla infundibuliform, the lobes arachnoid-villous within . . . . . 24. *Fernaldia*
zz. Corolla salverform, the lobes not arachnoid-villous within . . . . . 25. *Echites*
yy. Corolla with ligular appendages near the level of stamen attachment, the orifice with a callous or annular ring . . . . . 26. *Prestonia*
ss. Calyx lobes without squamellae basally . . . . . 27. *Rhabdadenia*

ARTIFICIAL KEY TO GENERA

a. Leaves alternate or spiral.
b. Corolla relatively small, the tube < 5 mm long (in Panama); follicle large, woody, compressed laterally, ca. 10 cm wide; seeds peltate, with a large, ca. 9–10 mm wide, concentric wing . . . . . 7. *Aspidosperma*
bb. Corolla mostly large and showy, the tube > 15 mm long; berries or follicles not conspicuously large or woody and not compressed laterally; seeds with eccentric wings, or if wings concentric, then not 9–10 mm wide.
c. Bracts conspicuous, ca. 13–17 mm long; calyx-lobes 4 or 5, small, < ca. 2.5 mm long; seeds with ± concentric wings . . . . . 6. *Himatanthus*
cc. Bracts minute; calyx lobes 5, ± equal; seeds with or without a basal wing.
d. Stems with conspicous leaf scars; calyx without squamellae; fruit a follicle; seeds winged basally . . . . . 5. *Plumeria*
dd. Stems without conspicuous leaf scars; calyx with squamellae; fruit a berry; seeds not winged . . . . . 12. *Thevetia*
aa. Leaves opposite, ternate, or quadrate.
e. Leaves ternate or quadrate.
f. Leaves ternate, mostly lanceolate.
g. Corolla small, salverform, the tube ca. 3–5 mm long, without appendages; seeds ciliate marginally . . . . . 8. *Tonduzia*
gg. Corolla showy, infundibuliform, the tube and throat ca. 17–20 mm long, appendaged; seeds densely pubescent and comose apically . . . . . 21. *Nerium*
ff. Leaves mostly quadrate, elliptic to obovate.
h. Inflorescences few-flowered; flowers large and showy; fruit a spiny capsule . . . . . 15. *Allamanda*
hh. Inflorescences many-flowered; flowers small; fruit a small drupe . . . . . 13. *Rauvolfia*
ee. Leaves opposite.
i. Leaves without glands either at the base of the midrib or along its entire length.
j. Leaves peltate . . . . . 22. *Peltastes*
jj. Leaves not peltate.
k. Vines or lianas, usually slender except in some species of *Prestonia*.
l. Flowers with a combination of long slender corolla and small, thin calyx-lobes . . . . . 25. *Echites*
ll. Flowers without the above combination.
m. Corolla appendaged within . . . . . 26. *Prestonia*
mm. Corolla not appendaged within.
n. Inflorescences mostly 2-flowered; calyx-lobes without squamellae . . . . . 27. *Rhabdadenia*
nn. Inflorescences several-flowered; calyx-lobes with squamellae.

o. Flowers mostly large and showy; stamens connivent and agglutinated to the stigma; leaves glabrous, or if pubescent the hairs without multicellular bases.
p. Squamellae alternate with the calyx-lobes or irregularly distributed; corolla throat without a thick indument ..... 23. *Odontadenia*
pp. Squamellae opposite the calyx-lobes; corolla throat ± closed by a thick indument ... 24. *Fernaldia*
oo. Flowers relatively small; stamens free and not agglutinated to the stigma; leaves pubescent, the hairs stiffened and with multicellular bases. . . . .
..... 11. *Anechites*
kk. Shrubs or herbs.
q. Herbs, mostly slender.
r. Corolla salverform; flowers 1–3 in the axils of leaves; annuals ..... 9. *Lochnera*
rr. Corolla infundibuliform; flowers single in the axils of leaves; perennials ..... 10. *Vinca*
qq. Shrubs.
s. Inflorescences few-flowered, axillary umbells; flowers small ..... 20. *Malouetia*
ss. Inflorescences many-flowered or if few-flowered, then not axillary umbells; flowers mostly large and showy except in some species of *Tabernaemontana*.
t. Calyx-lobes without squamellae; fruit a berry; seeds 1–4 ..... 14. *Lacmellea*
tt. Calyx-lobes with squamellae; fruit a follicle; seeds numerous.
u. Calyx-lobes large and foliaceous, 3–25 mm long, imbricate, mostly unequal, the outer 2 smaller, the inner 3 larger ..... 4. *Stemmadenia*
uu. Calyx-lobes mostly small, < 6 mm long, not imbricate, ± equal.
v. Leaves large, at least some 20–30 cm long, the midrib 1–2 mm high near the base beneath; corolla tube inflated near the base; follicles somewhat spherical ..... 1. *Bonafousia*
vv. Leaves, smaller, mostly < 20 cm long, the midrib not enlarged vertically; corolla tube cylindrical; follicles stout, but not spherical.
w. Flowers double, or if single, then the corolla tube 20–22 mm long .... 3. *Ervatamia*
ww. Flowers single, the corolla tube < 16 mm long ..... 2. *Tabernaemontana*
ii. Leaves with glands at the base of the midrib or scattered along its entire length.
x. Vines; flowers ± showy.
y. Leaf bases hastate or cordate; glands distributed along the entire length of the midrib ..... 18. *Mandevilla*
yy. Leaf bases ± obtuse; glands at the base of the midrib only.
z. Slender vines; glands 1 or 2 at the base of the midrib, deltoid; corolla tube cylindrical ..... 17. *Mesechites*
zz. Woody vines; glands numerous (> 4) at the base of the midrib; corolla tube inflated basally ..... 16. *Allomarkgrafia*
xx. Shrubs; flowers small ..... 19. *Forsteronia*

1. BONAFOUSIA

Bonafousia A. DC., Prodr. 8: 359. 1844.

Shrubs or trees, the stems cylindrical or sharply angled, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved, mostly subcoriaceous; petiolate, usually glandular in the axils. *Inflorescence*s cymose, few-flowered, sometimes reduced to a single flower, axillary. *Flowers* medium-sized; calyx 5-lobed, or sometimes connate basally, the lobes somewhat unequal, bearing squamellae within; corolla salverform to subsalverform, without appendages, the limb 5-lobed, sinistrorsely convolute; stamens 5, included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecuim 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectary adherent to the ovary, the style 1, the stigma pentagonal-umbraculiform. *Fruit* apocarpous, follicular, spherical to subspherical; seeds many, naked, embedded in a fleshy aril.

A genus of about nine species, mostly in northeastern South America; two species extend north into Panama.

Markgraf (Notizbl. Bot. Gart. Berlin-Dahlem 14: 151–184. 1938) resurrected several genera which had been reduced to *Tabernaemontana* L. The validity of all the genera which Markgraf recognized and separated from *Tabernaemontana* is questionable, but judging from the Panamanian material, *Bonafousia* deserves generic status.

a. Stems sharply angled; leaves ovate, at least some > 20 cm long; corolla tube twisted ..... 1. *B. sananho*
aa. Stems terete; leaves elliptic, < 15 cm long; corolla tube not twisted .... 2. *B. undulata*

1. **Bonafousia sananho** (Ruiz & Pavon) Markgraf, Notizbl. Bot. Gart. Berlin-Dahlem 14: 166. 1938.—FIG. 1.

Tabernaemontana sananho Ruiz & Pavon, Fl. Peru. 2: 22, *pl. 144*. 1799.

Shrubs, or trees to 7 m, the stems glabrous, sharply angled. *Leaves* elliptic to ovate, shortly acuminate, obtuse basally, to 40 cm long and 18 cm wide, glabrous, firmly membranaceous, the midrib enlarged vertically, especially near the base; petioles stout, ca. 1 cm long, weakly perfoliate. *Inflorescences* cymose, axillary, much smaller than the subtending leaves, the peduncle ca. 5–10 mm long. *Flowers* with the pedicels 2–10 mm long; bracteoles ovate and keeled, ca. 2–3 mm long; calyx lobes slightly unequal, oblong, ca. 6–10 mm long, bearing numerous squamellae within; corolla subsalverform, white with yellow lobes, the tube 17–20 mm long, slightly inflated near the base and constricted near the level of stamen attachment, the lobes obliquely dolabriform, ca. 8–9 mm long; stamens wholly included, attached about ⅔ the distance from the base, the anthers ca. 3.5–4 mm long. *Fruit* follicular, almost spherical, ca. 3.5 cm in diameter; seeds ovoid, ca. 1 cm long, the testa sulcate.

Panama, Colombia, Ecuador, Peru, and western Brazil.

BOCAS DEL TORO: Region of Almirante, *Cooper 610* (US). COCLE: Summit of Cerro Pilón, *Duyer et al. 4502b* (MO); site area of WEPCOR, *Kirkbride 1047, 1080* (both MO). PANAMA: Altos del Río Pacora, *Lewis et al. 2297* (MO). Cerro Campana, trail to mountain with cross, *Kirkbride 243* (MO).

A curious mixture of characteristics will separate *Bonafousia sananho* from the remaining Panamanian Apocynaceae—the very large leaves, which, in Panama, always seem to have a leafy liverwort and frequently a black mold associated with them, and the vertically enlarged midrib.

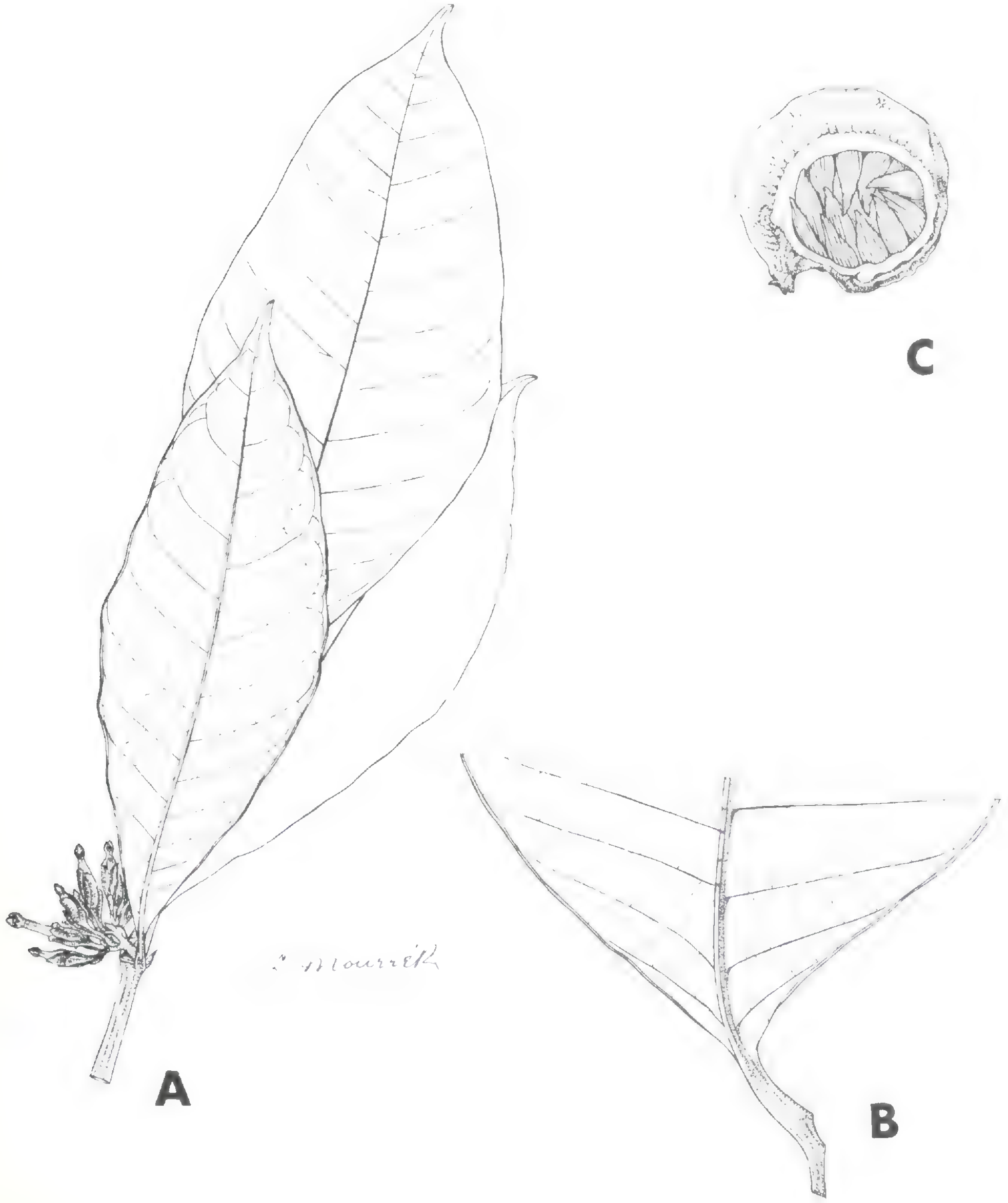

FIGURE 1. *Bonafousia sananho* (Ruiz & Pav.) Markgraf.—A. Habit (× 2/5). B. Basal portion of leaf showing vertically enlarged midrib (× 4/5).—C. Fruit in longitudinal section with seeds (× 4/5). [A, after *Duyer et al. 4502b* (MO); B C, after *Kirkbride et al. 243* (MO).]

2. **Bonafousia undulata** (Vahl) A. D.C., Prodr. 8: 359. 1844.

Tabernaemontana undulata Vahl, Eclog. Amer. 2: 20. 1798.

Shrubs, to ca. 3 m, glabrous, the stems terete. *Leaves* elliptic, acute, the margins undulate, obtuse basally, to 13 cm long and 5 cm wide, glabrous, firmly membranaceous, lustrous above and dull beneath; petioles indistinct, to ca. 1 cm long, weakly perfoliate, glandular in the axils. *Inflorescences* cymose, axillary (?), few-flowered. *Flowers* with the pedicels ca. 2–10 mm long; bracteoles not apparent; calyx-lobes slightly unequal, oblong-ovate, ca. 3–4 mm long; corolla salverform, rose to pink, the tube ca. 23 mm long, the lobes oblong-obovate (?); stamens included, attached ca. ⅔ the distance from the base, the anthers ca. 4 mm long; nectary adnate to the ovary, the stigma umbraculiform below and pentagonal above. *Fruits* unknown for Panama.

Panama, Trinidad, Guyana, nothern Brazil, and eastern Peru.

COLON: Santa Rita Ridge, ca. 10 mi. from Transisthmian Highway, *Porter et al. 4815* (MO).

Bonafousia undulata has never been reported from this far north before. Nevertheless I am fairly certain of the identity of this collection after a comparison with the type, *Ryan s.n.* (C, photo MO). The reduced description is due to a paucity of material.

2. TABERNAEMONTANA

Tabernaemontana L., Sp. Pl. 210. 1753.

Shrubs, or small trees, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved; petioles weakly perfoliate, ± glandular in the axils. *Inflorescences* cymose, compound, many-flowered, mostly axillary. *Flowers* small to medium-sized; calyx 5-lobed, the lobes equal, relatively small, bearing many squamellae; corolla salverform, without appendages, the tube straight, the limb 5-lobed, sinistrorsely convolute; stamens 5, included or ± exserted, attached midway or higher on the corolla tube, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectary shallow or absent, the style 1, the stigma umbraculiform below and capitate or pentagonal above. *Fruit* apocarpous, of 2 follicles, ± large and heavy; seeds many, naked, embedded in a fleshy aril.

A large genus of about 140 species in the American and African tropics.

Many genera, reduced by various authors to sections and subgenera of *Tabernaemontana*, have been resurrected and segregated by Markgraf (for a complete discussion, see Notizbl. Bot. Gart. Berlin-Dahlem 12: 540–552. 1935; 14: 151–184. 1938). I have treated the relevant Panamanian taxa as follows: *Bonafousia* and *Ervatamia* as distinct genera; *Peschiera* as synonomous with *Tabernaemontana*.

a. Anthers yellow throughout, inserted near or below the middle of the corolla tube, wholly included; internodes conspicuously short, the leaves tending to be crowded at the tips of branches ..... 1. *T. arborea*

aa. Anthers tinged with blue-green, inserted near the top of the corolla tube, sometimes partially exserted; internodes not conspicuously short, the leaves not crowded at the tips of branches.
b. Anthers half-exserted ..... 2. *T. amygdalifolia*
bb. Anthers included, or barely exserted ..... 3. *T. chrysocarpa*

1. **Tabernaemontana arborea** Rose *in* Donn. Sm., Bot. Gaz. (Crawfordsville) 18: 206. 1893. –Fig. 2.

Peschiera arborea (Rose) Markgraf, Notizbl. Bot. Gart. Berlin-Dahlem 14: 173. 1938.

Trees, to 20 m, the stems glabrous and slightly fistulose when young. *Leaves* elliptic to ovate-elliptic, acute to shortly acuminate, obtuse to attenuate basally,

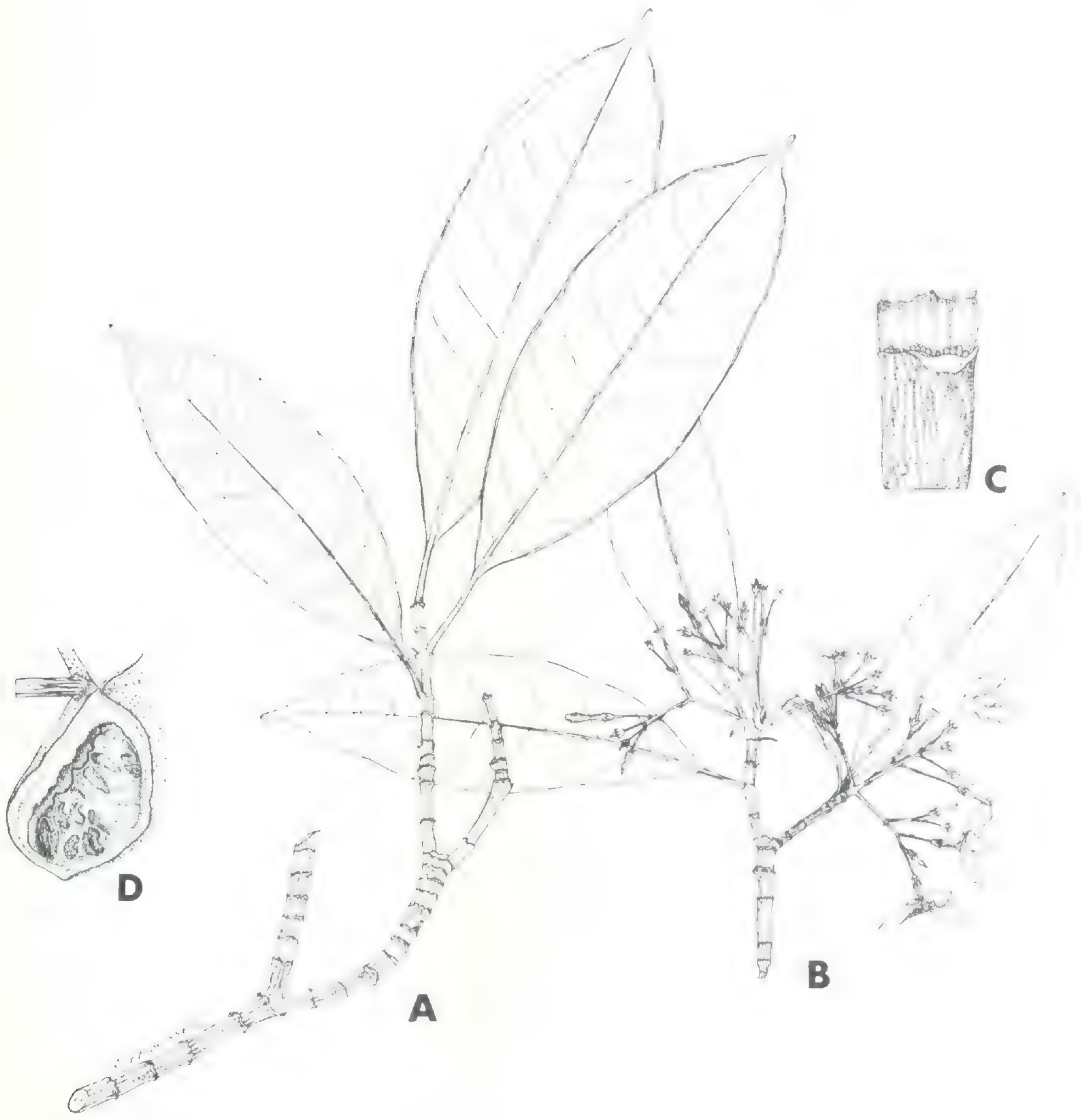

Figure 2. *Tabernaemontana arborea* Rose.—A. Habit (× ½).—B. Inflorescence (× ½).—C. Node with axillary glands (× 2 2/5).—D. Fruit in longitudinal section (× 3/5). [After *Croat* 8559 (MO).]

to 18 cm long and 6 cm wide, glabrous, firmly membranaceous; petioles to ca. 1 cm long, perfoliate when young and forming conspicuous rings on the stems, glandular in the axils. *Inflorescences* corymbose, sometimes broadly so, many-flowered, the peduncles short, the bracts not apparent. *Flowers* with the pedicels to 1 cm long; bracteoles present, variously placed, deltoid, ca. 1.5–2 mm long; calyx-lobes ovate, ca. 2–3 mm long, bearing several squamellae within; corolla white, the tube 6–8 mm long, pubescent within, the lobes obliquely ovate-oblong, ca. 10–13 mm long; stamens included, attached low in the corolla tube, the anthers ca. 2.5 mm long, yellow throughout; ovary without a nectary, the style short, ca. 1 mm long, the stigma 5-lobed. *Follicles* reniform, stout, to 6 cm long, the pericarp dull-brown and verrucose; seeds rugose, ± ovoid, ca. 10–12 mm long.

British Honduras, Guatemala, and Panama.

CANAL ZONE: Barro Colorado Island, *Croat 5241*, *5243*, *5419*, *7356*, *8120*, *8559* (all MO), *Shattuck 818* (F). Near Quebracho on Panama R.R., *Christopherson 123* (US). DARIEN: Manene to mouth of Río Cuási, *Kirkbride & Bristan 1393* (MO). PANAMA: Hills above Campana, *Allen & Alston 1862* (F, MO). Campana Hill, *Alston 8924* (F). SAN BLAS: Vicinity of Permé, *Cooper 283* (MO).

2. **Tabernaemontana amygdalifolia** Jacq., Enum. Syst. Pl. Carib. 14. 1760.

Shrubs, or small trees, to ca. 10 m, ± glabrous. *Leaves* elliptic to slightly obovate, acuminate, obtuse basally, to 18 cm long and 6 cm wide, chartaceous, glabrous; petioles ca. 5–15 mm long, weakly perfoliate, sparsely glandular in the axils. *Inflorescences* corymbose, generally much branched, open. *Flowers* with the pedicels 10–20 mm long; calyx lobes ovate, ca. 1.5–2 mm long, bearing several squamellae within; corolla white, the tube 12–15 mm long, slightly constricted at the insertion of the stamens, the lobes narrowly obovate-dolabriform, ca. 18–21 mm long; stamens half-exserted, the anthers ca. 2.2 mm long, tinged with blue-green; nectary annular, adnate. "Follicles narrowly ovoid ellipsoid, 3–6 cm. long, 1.25–1.8 cm. broad, narrowly acuminate, longitudinally striate, otherwise smooth."[3]

Southern Mexico, Central America, Colombia, and Venezuela.

PANAMA: Cerro Jefe, *Dressler 3752* (MO).

3. **Tabernaemontana chrysocarpa** Blake, Contr. Gray Herb. 52: 81. 1917.
T. pendula Woodson, Ann. Missouri Bot. Gard. 27: 331. 1940.

Shrubs, or small trees, to 10(–20) m, essentially glabrous. *Leaves* weakly obovate to elliptic, acuminate, obtuse basally, to 19 cm long and 8 cm wide, glabrous, chartaceous to ± membranaceous; petioles ca. 1–3 cm long, weakly perfoliate, mostly glandular in the axils. *Inflorescences* corymbose, pendant or lax, somewhat irregular, many-flowered, mostly axillary, the peduncle 3–13 cm long, the bracts apparently absent. *Flowers* with the pedicels ca. 7–15 mm long;

[3]The Panamanian collection was in flower only. The description of the fruit is quoted from Woodson, N. Amer. Fl. 29: 110–111. 1938.

bracteoles 1 or 2, ovate, scarious, ca. 1–1.5 mm long; calyx-lobes ovate, ca. 1.6–2.2 mm long, each bearing 4–5 squamallae; corolla white to green-yellow, the tube 7–9 mm long, slightly constricted at the insertion of the stamens, the lobes oblong-dolabriform, ca. 8–10 mm long; stamens barely exserted, attached near the top of the corrolla tube, the anthers ca. 2–2.5 mm long, tinged with blue-green; nectary very shallow, annular, the stigma pentagonal and umbraculiform. *Follicles* ovoid-subreniform, stout, coarsely ruminate when dry, ca. 2.5–4 cm long; seeds numerous, naked.

Central America.

BOCAS DEL TORO: Chiriquí Lagoon, Careening Cay, *von Wedel 2808* (MO, US); Colón Island, *von Wedel 111, 519, 4281* (all MO); Old Bank Island, *von Wedel 2089* (MO). COCLE: Between Cerro Pilón and El Valle de Antón, *Duke & Dwyer 13923, Dwyer & Correa 7930* (both MO). N of El Valle de Antón, *Allen 1734* (MO, holotype of *T. pendula*); trail to Las Minas, *Allen 2484* (MO). Vicinity of El Valle de Antón, *Allen 2076* (MO). Las Minas, *Allen 2703* (MO, US). DARIEN: Camp Teotuma, helipad in premontane rainforest, *Duke 15505* (MO). Río Chucunaque near Quebrada Boleillo, *Duke 8582* (MO).

3. ERVATAMIA

Ervatamia (A. DC.) Stapf, Fl. Trop. Africa 4(1): 126. 1904[1902].

Tabernaemontana sect. *Ervatamia* A. DC., Prodr. 8: 373. 1844.

Shrubs, rarely small trees, mostly glabrous, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved; petiolate, stipules axillary, ± glandular in the axils. *Inflorescences* cymose, corymbose, or umbelliform, terminal or pseudoaxillary and opposite, few to many flowered. *Flowers* small to moderately showy, sometimes double in cultivars; calyx 5-lobed, the lobes ± equal, each bearing several basal squamellae within; corolla salverform, yellow-green to white, without appendages, the tube straight, the limb 5-lobed, mostly sinistrorsely, rarely dextrorsely, convolute; stamens 5, included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectary absent (?), the style 1, the stigma fleshy below and bifid above. *Fruit* apocarpous, of 2 follicles, ± coriaceous, obliquely ovoid to lanceolate; seeds few to many, naked, embedded in a fleshy aril.

A genus of about 90 species found in the tropics of Asia, Australia, and Oceania.

Ervatamia, originally a section of *Tabernaemontana* L., was elevated to generic status by Stapf. Two species are known from Panama. *Ervatamia coronaria* (Jacq.) Stapf, which is widely cultivated in the tropics, occurs in its double-flowered form and is unlike the Panamanian species of *Tabernaemontana,* the other species, *E. cumingiana* (A. DC.) Markgraf, appears to be very similar to *Tabernaemontana* except for its longer corolla tube.

a. Flowers doubled; at least some leaves > 12 cm long . . . . . 1. *E. coronaria*
aa. Flowers single; most leaves < 10 cm long . . . . . 2. *E. cumingiana*

1. **Ervatamia coronaria** (Jacq.) Stapf, Fl. Trop. Africa 4(1): 127. 1904 [1902].

Nerium coronarium Jacq., Ic. Pl. Rar. 1: 5, *pl.* 52. 1781.

Shrubs, to ca. 1 m, the stems glabrous. *Leaves* elliptic, gradually acuminate, obtuse or attenuate basally, to 16 cm long and 6 cm wide, glabrous, firmly membranaceous; petioles 5–6 mm long or subsessile, weakly perfoliate, glandular in the axils, stipules small. *Inflorescences* cymose, sometimes reduced to a single flower, mostly axillary, the peduncle short, the bracts apparently absent. *Flowers* (in Panama, double) with the pedicels ca. 13–16 mm long; bracteole 1, deltoid, ca. 2 mm long, inserted near the middle of the pedicel; calyx-lobes slightly unequal, ovate, ca. 2–4 mm long, ciliate along the margins; corolla white, the tube ca. 18–22 mm long, glabrous within, thickened, the lobes ± 10, ca. 20 mm long; androecium, double or triple, the outer set epipetalous, the inner set(s) forming a tube, the anthers reduced and sterile; gynoecium apparently absent. *Fruits* unknown for Panama.

Native to India, but frequently cultivated and escaped in the tropics.

CANAL ZONE: Balboa, *Standley 30827* (US). Barro Colorado Island, *Croat 4629, 6008, Tyson 4201* (all MO). Mount Hope Cemetery, *Standley 28790* (US). Summit Gardens, *Steyermark,* 1935 (MO).

Due to the paucity of material, I have not dissected flowers from each of the collections cited above. However, all the specimens are similar, *i.e.* have double flowers, and undoubtedly represent a cultivated variety. Examination of Indian material [*Santapau 12882* (MO)] indicates the normal condition to be a 5-lobed corolla and 5 stamens attached on the tube about ⅔ the distance from the base.

2. **Ervatamia cumingiana** (A. DC.) Markgraf, Notizbl. Bot. Gart. Berlin-Dahlem 12: 547. 1935.—Fig. 3.

Tabernaemontana cumingiana A. DC., Prodr. 8: 373. 1844.

Shrubs, the stems glabrous. *Leaves* elliptic, gradually acuminate, obtuse basally, to 9 cm long and 2.5 cm wide, glabrous, firmly membranaceous; petioles 2–5 mm long, weakly perfoliate, glandular in the axils, the stipules small. *Inflorescences* corymbose, 6–15 flowered, axillary and opposite (?), the peduncle short. *Flowers* with the pedicels to 12 mm long; bracteoles minute, ca. 0.2 mm long, variously inserted; calyx-lobes ovate, ca. 1.2–1.5 mm long, bearing (1–)2(–3) squamellae within; corolla white, the tube ca. 19–22 mm long, glabrous within, the lobes obliquely obovate, ca. 15–18 mm long, stamens attached half way up the tube or higher, the anthers ca. 2 mm long; nectary absent, the stigma bifid above, the branches slender and appressed. *Fruits* unknown for Panama.

Native to India, but widely cultivated in the tropics.

CANAL ZONE: Balboa, *Standley 30831* (US). Government forest along Las Cruces Trail, *Hunter & Allen 750* (MO). Vicinity of Pedro Miguel, *Higgins 262* (US). PANAMA: Planted shrub in private garden near Panama City, *Sr. Hayden 68* (MO). Sabanas, *Bro. Paul 316* (MO).

FIGURE 3. *Ervatamia cumingiana* A. DC.—A. Habit (× 1 2/5).—B. Flower (× 1 2/5). [After *Hayden* 68 (MO).]

4. STEMMADENIA

Stemmadenia Benth., Bot. Voy. Sulphur 124, *pl. 44*. 1844.

Shrubs, or small trees, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved; petioles weakly perfoliate and ± glandular in the axils. *Inflorescences* cymose, or reduced racemes, terminal or pseudo-axillary, few-flowered. *Flowers* mostly large and showy; calyx 5-lobed, the lobes subequal to conspicuously unequal, mostly imbricate with the inner 3 larger, bearing many squamellae within; corolla salverform, subinfundibuliform, or infundibuliform, the tube or throat with 5 linear folds above the attachment of the stamens, the tube frequently twisted, the limb 5-lobed, sinistrorsely convolute; stamens 5, attached near the top of the tube or tube proper, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectaries concrescent and adnate to the ovary, the stigma umbraculiform below and capitate or biapiculate above. *Fruit* apocarpous, of 2 follicles, diverging, stout, leathery to slightly woody; seeds numerous, naked, embedded in a fleshy aril.

A genus of about 15 species in Mexico, Central America, northern South America, and Bolivia.

Woodson (Ann. Missouri Bot. Gard. 15: 341–373. 1928) gives adequate reasons for the separation of *Stemmandenia* from *Tabernaemontana* L. However, I do not agree with his subgeneric groupings—the shape of the corolla in many species is intermediate between salverform and infundibuliform, and the position of the bracts is not necessarily correlated in the manner described in his key.

a. Calyx lobes large and broadly ovate.
  b. Inflorescences pubescent; corolla definitely infundibuliform, the throat broadly conic ..... 1. *S. obovata*
  bb. Inflorescences glabrous; corolla salverform.
    c. Calyx-lobes ca. as long as the corolla tube or slightly shorter ..... 2. *S. donnell-smithii*
    cc. Calyx-lobes ca. half as long as the corolla tube or shorter ..... 3. *S. grandiflora*
aa. Calyx-lobes long and slender or rarely very short.
  d. Calyx-lobes small, < 5 mm long ..... 4. *S. alfari*
  dd. Calyx-lobes large, at least some > 6 mm long.
    e. Calyx-lobes 6–9 mm long; corolla tube proper ca. 10–12 mm long ... 5. *S. allenii*
    ee. Calyx-lobes 9 20 mm long; corolla tube proper > 15 mm long.
      f. Corolla throat 40–45 mm long ..... 6. *S. macrantha*
      ff. Corolla throat 12–15 mm long ..... 7. *S. lagunae*

1. **Stemmadenia obovata** var. **mollis** (Benth.) Woodson, Ann. Missouri Bot. Gard. 15: 358. 1928.

Stemmadenia mollis Benth., Bot. Voy. Sulphur 125. 1845.

Small *trees,* to 8 m, or shrubs, the younger stems brown-pubescent. *Leaves* elliptic to weakly obovate, shortly acuminate, obtuse basally, to 17 cm long and 9 cm wide, pubescent on both surfaces, densely so on the veins beneath, firmly membranaceous; petioles 3–7 mm long, pubescent, perfoliate, densely glandular in the axils. *Inflorescences* cymose, 1–6 flowered, terminal (?), the peduncle ca. 2.5 cm long. *Flowers* with the pedicels 5–10 mm long, pubescent; bracteoles 2–3,

unequal, ovate, 7–15 mm long, pubescent; calyx-lobes unequal, in 2 series, the outer 2 lobes shorter, ovate to oblong, 15–25 mm long, foliaceous; corolla infundibuliform, yellow, the tube proper ca. 20 mm long, pubescent within, the throat broadly conic, ca. 25 mm long, the lobes obliquely obovate, ca. 16–20 mm long; stamens attached at the orifice of the tube, the anthers ca. 4–4.5 mm long; nectary adnate to the ovary, the stigma capitate above and fleshy below. *Follicles* obovoid-subreniform, acuminate, ca. 4 cm long and 3 cm wide; seeds rugose, ca. 7–9 mm long.

Southern Mexico, Central America, Ecuador, and Bolivia.

LOS SANTOS: Las Tablas, *Allen 812* (F, US).

The collection cited above had only one flower, and additional material, *Rose et al. 9274* (MO) from Mexico and *Greenman & Greenman 5713* (MO) from Nicaragua, both determined by Woodson, were used to complete the description.

2. **Stemmadenia donnell-smithii** (Rose) Woodson, Ann. Missouri Bot. Gard. 15: 369. 1928.

Tabernaemontana donnell-smithii Rose, Bot. Gaz. (Crawfordsville) 18: 206. 1893.

Trees, to 28 m, the stems ± glabrous. *Leaves* elliptic to obovate, acuminate, obtuse basally, to 18 cm long and 7 cm wide, membranaceous, pubescent in the axils of the midrib and on the principal veins beneath; petioles ca. 5–8 mm long, weakly perfoliate and glandular in the axils. *Inflorescences* cymose, mostly terminal, 1–5 flowered. *Flowers* with the pedicels 5–9 mm long; bracteoles 3, unequal, ovate, ca. 2–6 mm long, inserted at the summit of the pedicel; calyx lobes ± unequal, in 2 series, the outer 2 lobes shorter, broadly ovate, 15–25 mm long, foliaceous; corolla salverform, yellow, the tube ca. 25–30 mm long, the lobes obliquely obovate, ca. 13–15 mm long; stamens attached ca. midway on the corolla tube, the anthers ca. 4.5–5 mm long; nectary low and annular. "*Follicles* about 3.5 cm. long, about 3 cm. broad, rounded at the apex."[4]

Mexico and Central America.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, Water Valley, *von Wedel 1379* (MO, US). CHIRIQUI: Cerro Galera Chorcha, *Allen 5022* (F, MO, US). Along highway near Río Tabasará, *Woodson et al. 411* (MO).

The calyx, with unequal lobes in two series, and the three rather large subtending bracts make *S. donnell-smithii* an easily recognized species. A small beetle appears to inhabit the flowers, since most collections contained at least one.

3. **Stemmadenia grandiflora** (Jacq.) Miers, Apoc. S. Amer. 75. 1878.

Tabernaemontana grandiflora Jacq., Enum. Syst. Pl. Carib. 14. 1760.

Shrubs, or small trees to 7 m, ± glabrous. *Leaves* elliptic to obovate, acuminate, obtuse to slightly rounded basally, to 16 cm long and 6 cm wide, glabrous

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[4]In the absence of Panamanian fruiting material, the description is quoted from Woodson, Ann. Missouri Bot. Gard. 15: 369. 1928.

on both surfaces or pubescent on the veins beneath, membranaceous; petioles 2–10 mm long. *Inflorescences* cymose, 2–9-flowered, mostly axillary, the peduncles ca. 3–10 mm long, the bracts apparently absent. *Flowers* with the pedicels 4–9 mm long; bracteole 1, ovate, ca. 1.5–2 mm long, attached ca. midway on the pedicel; calyx lobes unequal, ovate to oblong-ovate, foliaceous, 12–20 mm long and 4–15 mm wide, bearing numerous squamellae within; corolla salverform, yellow, the tube 22–35 mm long, pubescent within at the level of stamen attachment, the lobes obliquely-obovate, 20–25 mm long; stamens included, attached ca. ⅔ the way up the corolla tube, the anthers ca. 4 mm long; nectary annular, adnate to the ovary and shallow. *Follicles* obovoid-subreniform, stout, 2–3 cm long; seeds many, verrucose, ca. 5–7 mm long.

Mexico, Nicaragua, Costa Rica, Panama, and northern South America.

BOCAS DEL TORO: Water Valley, *von Wedel 960* (MO). CANAL ZONE: Albrook AFB Research Forest Site, *Mowbray et al. 5208* (MO). Barro Colorado Island, *Croat 4223, 4393, 4620, 6003, 6134, 6146, 7086, Ebinger 275, Sr. Hayden 88* (all MO), *Woodworth & Vestal 506* (F). Near Corozal, *Allen 913* (MO). Farfan Beach area, *Tyson 1836* (MO). Fort Clayton near SCN-TV, *Tyson & Blum 3899* (MO). Madden Dam, Saddle 11 near Alahuela, *Dodge et al. 16511* (MO); entrance to Boy Scout Camp, *Dwyer & Sr. Hayden 24* (MO); area near Transisthmian Highway, *Stern et al. 41* (MO). Vicinity of Miraflores Lake, *P. White 76* (MO); lower end of island, *P. White 115* (MO). 1 mi. NE of Piña, *Lewis et al. 1840* (MO). Vicinity of Río Providencia, 12 mi. S of Colón, *Blum & Tyson 2333* (MO). CHIRIQUI: 2 mi. SW of Guabala, *Tyson et al. 4255* (MO). COCLE: El Valle de Antón, *Hunter & Allen 369, Siebert 423* (both MO). On old road to coast, 1.5 mi. S of Antón, *Tyson & Blum 2587* (MO). COLON: María Chiquita, E of Río Piedras toward Portobelo, *Dwyer & Kirkbride 7779* (MO). DARIEN: Vicinity of Caná, *Stern et al. 701* (MO). Vicinity of Chepigana, *Duke & Bristan 263* (MO). Vicinity of Paya, Río Paya, *Stern et al. 189, 218* (both MO). Río Balsa between Río Areti and Manene, *Duke 8763* (MO). Clearing at confluence of Río Chucunaque & Río Canclones, *Duke 5124* (MO). Río Tucutí between Tucutí Río and Río Uroganti, *Duke 5283* (MO). Near mouth of Río Yapé, *Allen 365* (MO). HERRERA: Road between Las Minas & Pesé *Duke 12304* (MO). 21.5 mi. S of Ocú, *Lewis et al. 1650* (MO). LOS SANTOS: Between Los Santos & Guarare, *Woodson et al. 1198* (MO). Río Tonosí, vicinity of Tonosí, *Lewis et al. 1538* (MO). Road between Tonosí & Guanico, *Stern et al. 1879* (MO). 10 mi. N of Tonosí, *Tyson et al. 2951* (MO). PANAMA: Thickets & forests near Arraijan, *Woodson et al. 1363* (MO). Cerro Jefe, *Dwyer et al. 7297* (MO). Chepo Road and Pacora Road, *Correa & Dressler 446* (MO). Wet savanna E of Pacora, *Woodson et al. 736* (MO). Pedro Gonzales Island, *Allen 2591* (MO). Río Tatare, *Woodson & Schery 1000* (MO). San José Island, *Duke 12568* (MO). Taboga Island, *Woodson et al. 1514* (MO). Taboguilla Island, *Duke 5879* (MO). SAN BLAS: Soskatupu Island, *Duke 8941, 15477, Elias 1682* (all MO). VERAGUAS: 5 mi. NE of La Mesa, *Blum & Tyson 634* (MO). 5 mi. E of Santiago, *Tyson et al. 4276* (MO).

4. **Stemmadenia alfari** (Donn. Sm.) Woodson, Ann. Missouri Bot. Gard. 15: 360. 1928.

Tabernaemontana alfari Donn. Sm., Bot. Gaz. (Crawfordsville) 24: 396. 1897.

Small *trees*, to 4 m, the stems glabrous. *Leaves* elliptic, acuminate, obtuse basally, to 12 cm long and 5 cm wide, glabrous, membranaceous; petioles 3–5 mm long, weakly perfoliate, glandular in the axils. *Inflorescences* racemose, pseudo-axillary (?), few-flowered, the peduncle ca. 2–4 mm long. *Flowers* with the pedicels ca. 1–4 mm long; bracteole 1, deltoid, ca. 1.5 mm long; calyx-lobes subequal, ovate, ca. 3–4 mm long, glabrous, each bearing 4–6 oppositely placed squamellae within; corolla subinfundibuliform, orange to yellow, the tube proper ca. 10 mm long, the throat narrowly conic, ca. 15 mm long, the lobes obliquely

obovate, ca. 9–12 mm long, spreading; stamens attached at the top of the corolla tube, the anthers ca. 4–4.2 mm long; nectaries concrescent and adnate to the ovary, the stigma capitate above and umbraculiform below. *Follicles* slender, curved, acuminate, ca. 3–5 cm long and 1–1.3 cm broad; seeds unknown.

Costa Rica and Panama.

COCLE: N rim of El Valle de Antón, *Allen 1783* (F, MO, US). El Valle site area of WEPCOR, *Kirkbride 1044* (MO).

Stemmadenia alfari is easily separated from the remaining Panamanian members of this genus by its small calyx lobes.

5. **Stemmadenia allenii** Woodson, Ann. Missouri Bot. Gard. 28: 461. 1941.—FIG. 4A.

Trees or shrubs, to 4 m, ± glabrous. *Leaves* elliptic, acuminate, obtuse basally, to 14 cm long and 6 cm wide, glabrous, membranaceous; petioles 3–7 mm long, weakly perfoliate. *Inflorescences* cymose, axillary, 1–4 flowered. *Flowers* with the pedicels ca. 4–5 mm long; bracteole 1, deltoid, attached ca. midway on the pedicel; calyx-lobes unequal, oblong, ca. 6–9 mm long, glabrous; corolla infundibuliform, pale yellow to white, the tube proper 10–12 mm long, the throat 15–20 mm long, the lobes obliquely obovate, ca. 12–15 mm long; stamens attached at the top of the corolla tube, the anthers ca. 3 mm long; nectaries somewhat fleshy, the stigma umbraculiform-pentagonal. *Follicles* slender, strongly divergent, both ends acuminate, ca. 3–5 cm long; seeds compressed, ovate, ca. 7–9 mm long, the testa rugose.

Known only from Panama.

COCLE: Cerro Pilón at El Valle de Antón, *Duke 12159, Dwyer & Correa 7936, Dwyer et al. 4502a, Porter et al. 4628* (all MO). N of El Valle de Antón, *Allen 2187* (MO, holotype), *2239, 3692* (both US). Vicinity of La Mesa, N of El Valle de Antón, *Allen 2364* (MO, US). PANAMA: Between Cerro Azul and Cerro Jefe, *Dressler 3333* (MO). Cerro Campana, *Dressler 3523, Sr. Hayden 116, Dwyer & Kirkbride 7848* (all MO).

6. **Stemmadenia macrantha** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 253. 1929.

Tree, to 8 m, the stems glabrous. *Leaves* elliptic to weakly obovate, acuminate, obtuse basally, 8–11 cm long and 2–3.5 cm wide, glabrous, membranaceous; petioles ca. 2–4 mm long, weakly perfoliate and glandular in the axils. *Inflorescences* racemose, axillary, the peduncle ca. 3 mm long. *Flowers* with the pedicels 2–4 mm long; bracteoles not apparent; calyx-lobes unequal, slender and oblong, ca. 10–22 mm long and 2–4 mm wide, glabrous; corolla subinfundibuliform, yellow, the tube proper ca. 23 mm long, the throat narrowly conic, ca. 40–45 mm long, the lobes obliquely obovate, ca. 25–30 mm long; stamens attached at the top of the corolla tube, the anthers ca. 4.2 mm long. *Follicles* unknown.

Known only from the type collection.

BOCAS DEL TORO: Kankintoe, 10 mi. above Holstein, *Cooper 510* (F, holotype, US, isotype).

A description of the ovary and surrounding structures was omitted due to a paucity of material. Additional collections may prove that *S. macrantha* and *S. lagunae* Woodson are conspecific; only the length of the corolla throat separates the two species.

7. **Stemmadenia lagunae** Woodson, Ann. Missouri Bot. Gard. 29: 364. 1942. —FIG. 4B.

Trees, to 13 m, the stems ± glabrous. *Leaves* elliptic to weakly obovate, acuminate, obtuse basally, to 15 cm long and 6 cm wide, glabrous on both surfaces, or pubescent along the midrib beneath, membranaceous; petioles 3–5 mm long, weakly perfoliate and sparsely glandular in the axils. *Inflorescences* racemose, bostrychoid, terminal to subterminal, few-flowered, the peduncle short, < 5 mm long. *Flowers* with the pedicels 3–5 mm long; bracteole 1, minute, scarious; calyx-lobes unequal, oblong, ca. 6–20 mm long and 2–4 mm wide, glabrous; corolla subinfundibuliform, yellow, the tube proper 20–22 mm long, the throat narrowly conic, ca. 12–15 mm long, the lobes obliquely obovate, ca. 15–20 mm long; stamens attached at the top of the corolla tube, the anthers ca. 4 mm long. *Follicles* unknown.

Apparently only from Panama.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, Colón Island, *von Wedel 570* (MO, holotype); Fish Creek Mts., *von Wedel 2247* (US); Water Valley, *von Wedel 587, 1048* (both MO).

The paucity of good flowering material and the maltreated type collection have precluded a description of the ovary and surrounding structures.

5. PLUMERIA

Plumeria L., Sp. Pl. 209. 1753.

Trees, small, or shrubs, the stems corky and fistulose, lacticiferous. *Leaves* spiral or alternate, clustered at the ends of branches, non-glandular, pinnately nerved; petiolate or subsessile, glandular or non-glandular in the axils. *Inflorescences* corymbose to thyrsiform, sometimes fastigiately so, the secondary peduncles mostly terminal, frequently developed, few- to many-flowered. *Flowers* large and showy; calyx 5-lobed, the lobes equal to subequal, usually small, without squamellae; corolla salverform or sometimes subinfundibuliform, thick and waxy, white to red, without appendages, 5-lobed, sinistrorsely convolute; stamens 5, wholly included, attached near the base of the corolla tube, the anthers not connivent and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary subinferior, the ovules numerous, without a nectary, the style 1, short, the stigma slenderly bicapitate, almost sessile. *Fruit* apocarpous, of 2 follicles, coriaceous or woody; seeds numerous, dry, flattened, winged basally, the wing large and irregular.

A genus of about eight species in southern Mexico, Central America, the West Indies, and nothern South America.

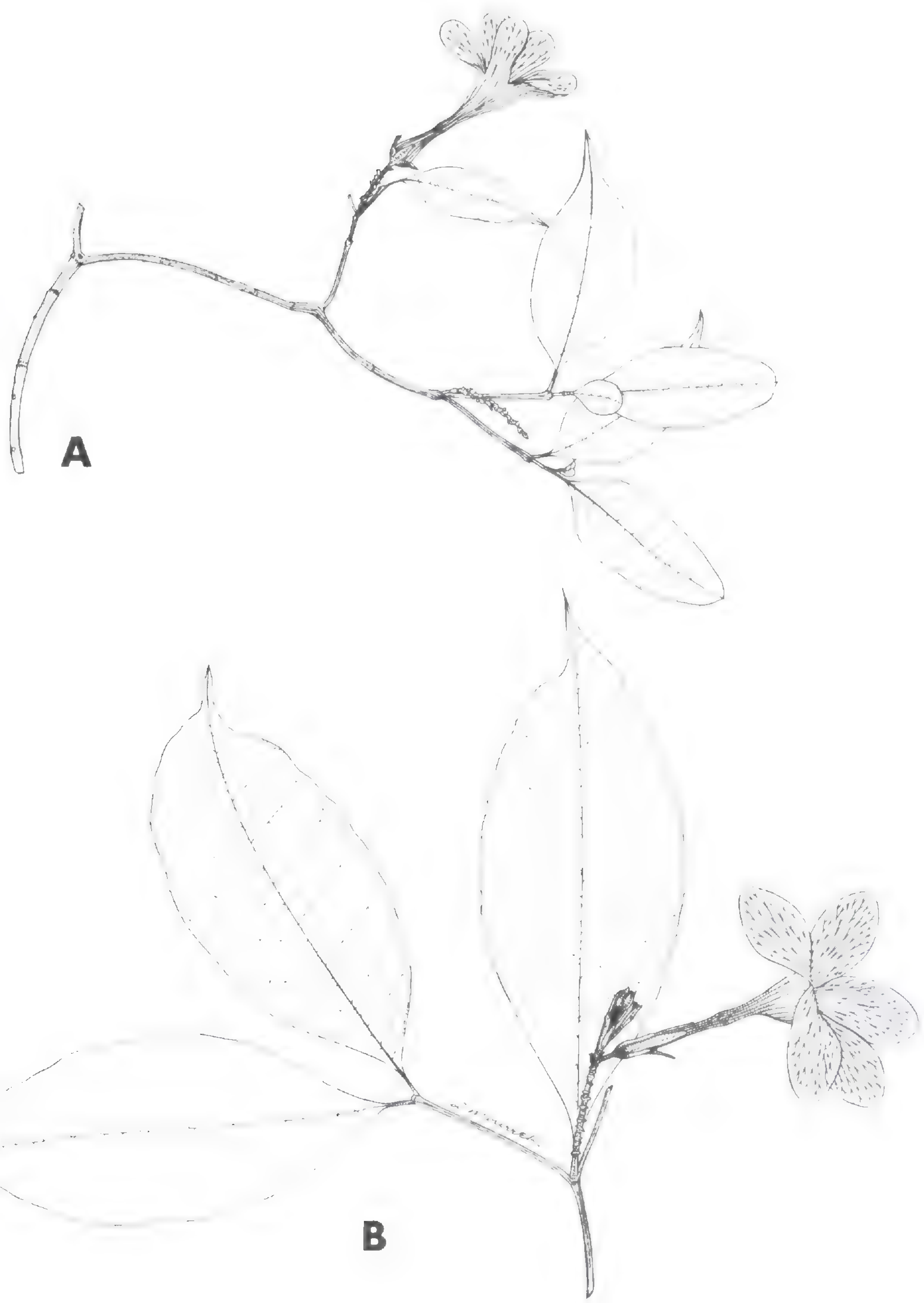

FIGURE 4. *Stemmadenia.*—A. S. *allenii* Woodson, flowering branch (× 7/10). [After *Allen 2364* (MO).]—B. *S. lagunae* Woodson, flowering branch (× 7/10). [After *von Wedel 570* (MO).]

Plumeria is widely cultivated in the tropics and subtropics of both hemispheres because of its attractive and showy flowers.

Useful reference:

Woodson, R. E., Jr. An evaluation of the genera *Plumeria* L. and *Himatanthus* Willd. Ann. Missouri Bot. Gard. 25: 189–224. 1938.

a. Leaves elongate-rhomboid ..... 1. *P. pudica*
aa. Leaves obovate to oblong-elliptic ..... 2. *P. rubra*

1. **Plumeria pudica** Jacq., Select. Stirp. Amer. Hist. 1: 37. 1763.—FIG. 5.

Shrubs, to 3.5 m, the leaf scars pronounced. *Leaves* elongate-rhomboid, sometimes almost lobed when immature, acute, attenuate basally, to 22 cm long and 6 cm wide, glabrous above, pubescent on the veins beneath, the principal veins weakly anastomising and forming a marginal vein; subsessile, sparsely glandular in the axils. *Inflorescences* cymose, the secondary peduncles usually developed, many-flowered, terminal, the primary peduncle to 7 cm long. *Flowers* with the pedicels 8–12 mm long; bracteoles present, deltoid, ca. 1.5–2 mm long; calyx-lobes deltoid, fleshy, ca. 1.5–2 mm long, glandular (?) tipped; corolla slightly subinfundibuliform, white, sometimes with a yellow center, the tube ca. 20–25 mm long, pubescent within, the lobes broadly ovate, ca. 30 mm long; anthers ca. 2 mm long; stigma somewhat fleshy below and slenderly bicapitate above. *Follicles* ca. 5–10 cm long; seeds unknown.

Panama, Martinique, Colombia, and Venezuela.

PANAMA: San José Island, *Erlanson* 55 (US). Cerro Campana, *Fairchild & Allen 1163* [cultivated at Fairchild Gardens, voucher *Gillis* 8267 (Herbarium Fairchild Tropical Gardens)].

2. **Plumeria rubra** L., Sp. Pl. 209. 1753.—FIG. 6.

Trees, to 25 m, the stems corky, the leaf scars pronounced, the younger parts softly pubescent. *Leaves* obovate to ± oblong-elliptic, acute, obtuse basally, to 40 cm long and 15 cm wide, mostly glabrous above, ± pubescent beneath especially near the midrib, the secondary veins anastomosing and forming a lateral vein, firmly membranaceous; petioles stout, sparsely pubescent, ca. 3–7 cm long. *Inflorescences* corymbose, mostly terminal, the peduncles to 12 cm long. *Flowers* with the pedicels 0.4–2 cm long, pubescent; bracts minute; calyx-lobes ovate-quadrate, weakly mucronate, pubescent, ca. 1 mm long; corolla salverform, white, flushed with pink beneath, sometimes with a yellow throat, the tube ca. 14–18 mm long, pubescent within, the lobes broadly obovate, 30–45 mm long and 15–25 mm wide; anthers ca. 2 mm long. *Follicles* compressed, 20–30 cm long and 2–3 cm wide; seed proper 2.8–3 cm long, the wing 3–4 cm long.

Southern Mexico, Central America, the West Indies, and widely cultivated in the tropics of both hemispheres.

BOCAS DEL TORO: Water Valley, *von Wedel 645* (MO). CANAL ZONE: Between Farfan Beach and Vera Cruz, *Duke 11729* (MO). PANAMA: Taboga Island, *Allen 133* (MO), *Maxon 6914* (F). SAN BLAS: Mainland opposite Ailigandi, from mouth of Rio Ailigandi, to 2.5 mi. inland, *Lewis et al. 164* (MO). Mulatuppu, *Duke 8549* (MO).

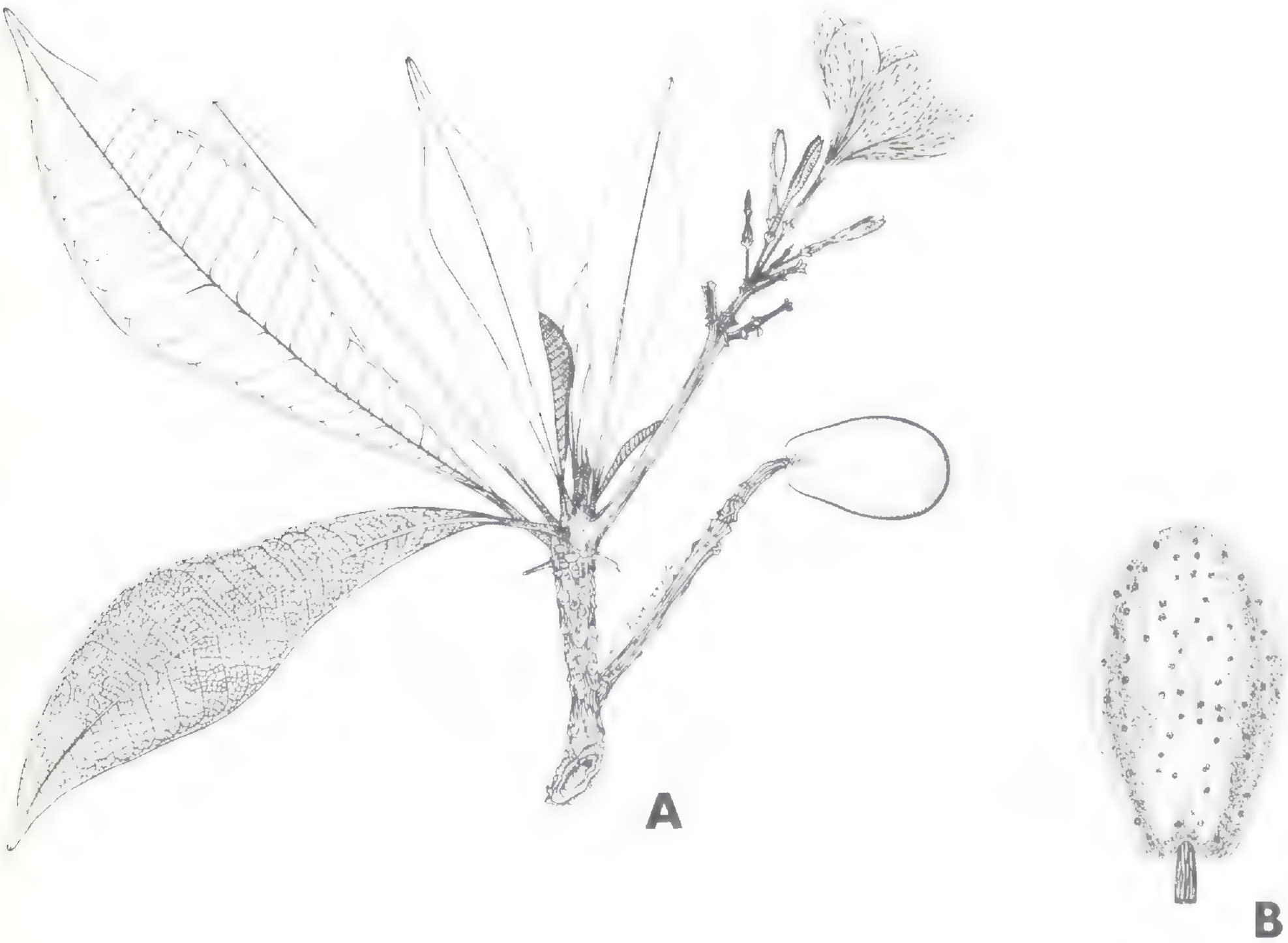

FIGURE 5. *Plumeria pudica* Jacq.—A. General habit with flower (× 3/10).—B. Open follicle (× 3/5). [After *Gillis* 8267 (Herbarium Fairchild Tropical Gardens).]

6. HIMATANTHUS

Himatanthus Willd. *ex* Roem. & Schult., Syst. 5: 221. 1819.

Trees, small to medium-sized, the stems somewhat fistulose, lactescent. *Leaves* alternate, non-glandular, pinnately-nerved; petiolate, sparsely glandular in the axils. *Inflorescences* thyrsiform, mostly terminal, several to many flowered. *Flowers* mostly large; bracts conspicuous, foliaceous or petaloid, caducous, glandular in the axil; calyx 1–5 lobed, the lobes unequal and reduced, sometimes obsolete, without squamellae within; corolla salverform, white, without appendages, the tube straight, the limb 5-lobed, the lobes sinistrorsely convolute; stamens 5, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary subinferior, the ovules numerous, nectaries absent, the style 1, the stigma fusiform below and biapiculate above. *Fruit* apocarpous, of 2 follicles, somewhat compressed; seeds numerous, dry, ± concentrically winged.

A genus of seven species in northern South America; one species extends into southern Panama.

Useful reference:

Woodson, R. E., Jr. An evaluation of the genera *Plumeria* L. and *Himatanthus* Willd. Ann. Missouri Bot. Gard. 25: 189–224. 1938.

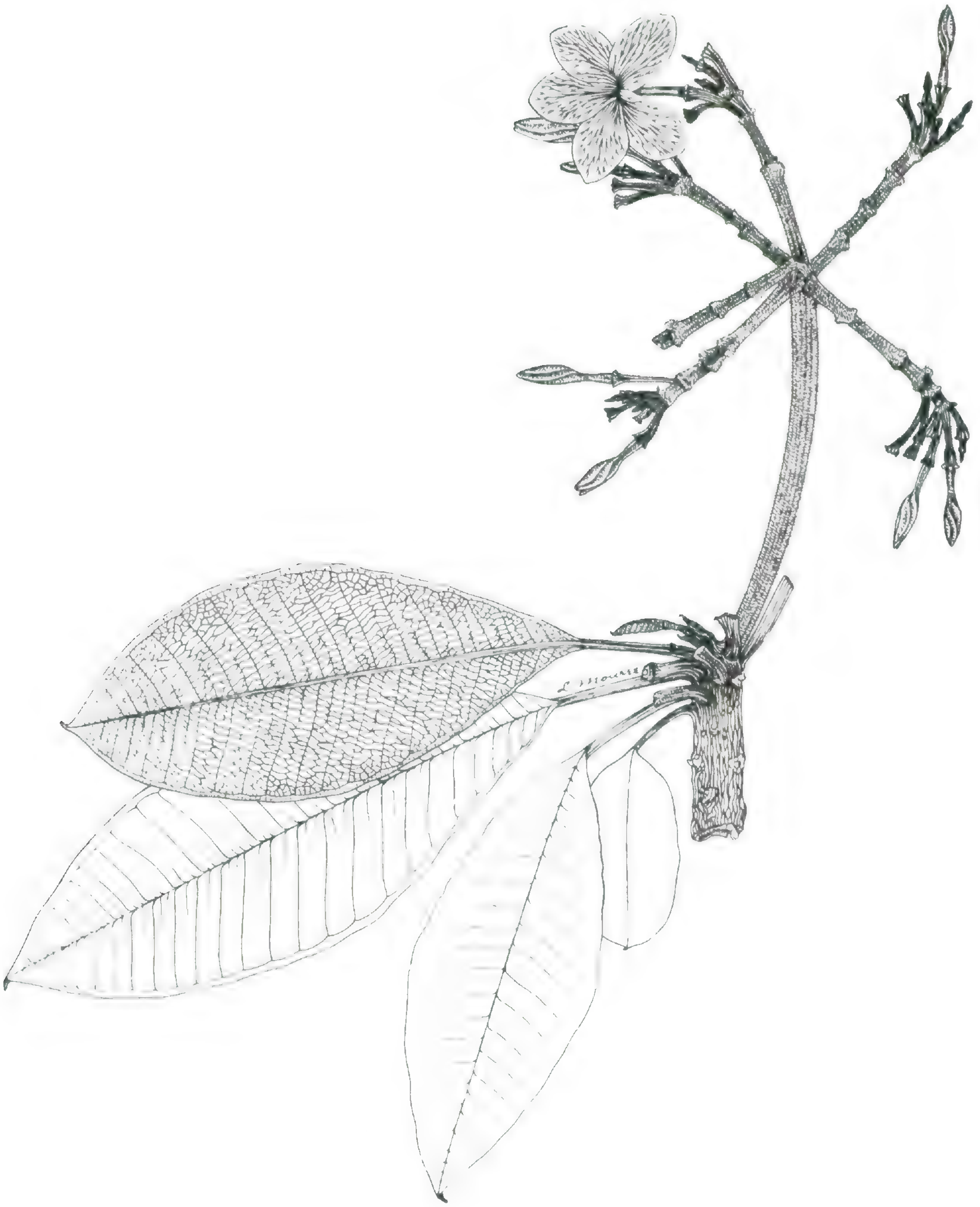

FIGURE 6. *Plumeria rubra* L., general habit with inflorescence (× 1/3). [After *Maxon 6914* (US).]

Himatanthus articulata (Vahl) Woodson, Ann. Missouri Bot. Gard. 25: 196. 1938.—FIG. 7.

Plumeria articulata Vahl, Eclog. Amer. 2: 2. 1798.
P. microcalyx Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 254. 1929.

Trees, to 10 m, ± glabrous. *Leaves* obovate, acute, obtuse to attenuate basally, to 25 cm long and 9 cm wide, glabrous, firmly membranaceous, lustrous above and dull beneath; petioles ca. 1.5–3 cm long. *Inflorescences* thyrsiform, regularly branched, terminal. *Flowers* with the pedicels 3–6 mm long; bracts broadly ovate, abruptly subcaudate-acuminate, 12–18 mm long; calyx-lobes 1–3, unequal, 0.5–2 mm long on the same flower; corolla-tube ca. 18–20 mm long, pubescent within, the lobes obovate-oblong, 22–25 mm long; stamens included, attached near the base of the corolla tube, the anthers ca. 2 mm long. *Follicles* stout, compressed laterally, ca. 20 cm long; seeds ca. 7 cm long.

Panama and northeastern South America.

COLON: Caná and vicinity, *Williams 823* (NY). DARIEN: Piriaque camp at river, *Tyson et al. 4771* (MO). Río Balsa, between Manene and Tusijuanda, *Duke 13560* (MO). Vicinity of Río Paya, *Stern et al. 185* (MO, US). SAN BLAS: Permé, *Cooper 642* (F, holotype of *Plumeria microcalyx*).

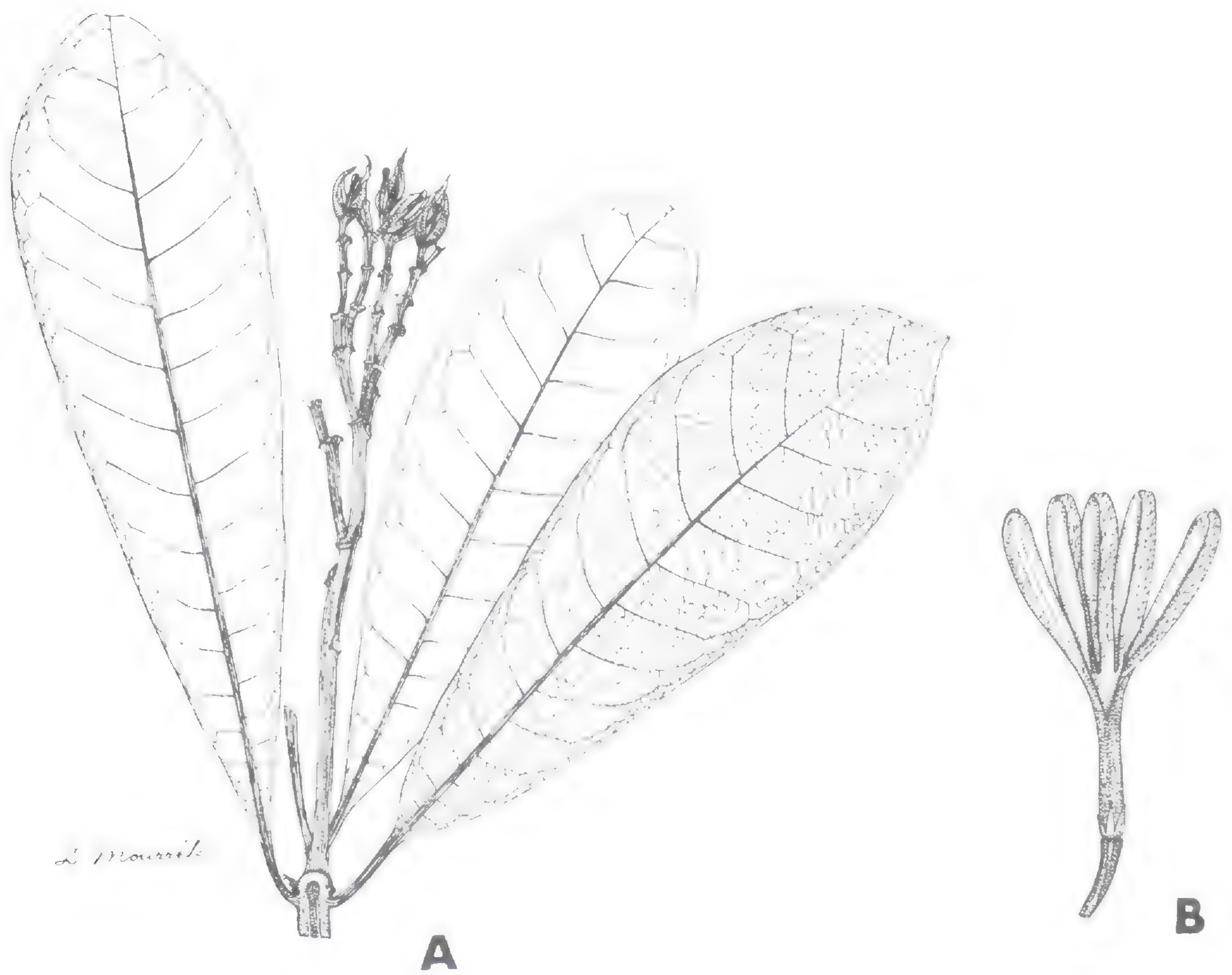

FIGURE 7. *Himatanthus articulata* (Vahl) Woodson.—A. Habit (× 1/3).—B. Partially dissected flower (× 1 ¼). [A, after *Duke 13560* (MO); B, after *Stern et al. 185* (MO).]

7. ASPIDOSPERMA

Aspidosperma Mart. & Zucc. *in* Mart., Nov. Gen. & Sp. 1: 57. 1824.
Cufodontia Woodson, Arch. Bot. Sist. 10: 39. 1934.

Trees or shrubs, lacticiferous, the latex white or reddish. *Leaves* alternate, rarely opposite and decussate, or ternate, non-glandular, pinnately-nerved; mostly petiolate. *Inflorescences* cymose to aggregate dichasial and thyrsiform, axillary or terminal, sometimes extra-axillary, the secondary peduncles frequently fasciculate in umbell-like form. *Flowers* small- to medium-sized; calyx 5-lobed, the lobes equal to conspicuously unequal, or rarely 4-lobed with the 2 outermost lobes connate and the 2 inner lobes free and included, without squamellae within; corolla salverform, tubular-salverform or tubular, the tube straight or inflated, terete or callose-angulate, the limb 5-lobed, sinistrorsely convolute; stamens 5, inserted midway or higher in the corolla tube, filamented, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, rarely reduced to 2, with or without a low annular nectary, the style 1, the stigma ± clavate to subcapitate. *Fruit* apocarpous, of 2 follicles, ± woody, mostly compressed, rarely cylindroid; seeds numerous, rarely reduced to 2, compressed, peltate, winged, the wing concentric or eccentric.

About 50 species in Mexico, Central America, Hispaniola and Trinidad, and most of South America.

Useful Reference:

Woodson, R. E., Jr. Studies in the Apocynaceae. VIII. An interim revision of the genus *Aspidosperma* Mart. & Zucc. Ann. Missouri Bot. Gard. 38: 119-206. 1951.

a. Corolla tube strongly callose-angulate, the lobes tightly spirally-contorted in bud . . . . . 1. *A. megalocarpon*
aa. Corolla tube essentially terete, the lobes erect or loosely spiral in bud . . . . 2. *A. darienense*

1. **Aspidosperma megalocarpon** Müll. Arg., Linnaea 30: 400. 1860. —FIG. 8.
A. cruentum Woodson, Amer. Jour. Bot. 22: 684. 1935, *"cruenta."*
A. sanguineum Bartlett, Publ. Carnegie Inst. Wash. 461: 16. 1935, *nom. nud.*
A. sanguinale Bartlett, *loc. cit.*, 22, *nom. nud.*

Trees, to 25 m, latex yellow to red, the younger stems minutely and densely pubescent. *Leaves* alternate, oblong-elliptic, acute, obtuse basally, to 26 cm long and 7 cm wide, glabrous, subcoriaceous, lustrous above and dull beneath; petioles ca. 1–3 cm long. *Inflorescences* corymbose-thyrsiform, axillary or terminal at the uppermost nodes, the bracts not apparent. *Flowers* with the pedicels 1–2 mm long; calyx 5-lobed, the lobes somewhat unequal, ovate, ca. 2 mm long, densely brown-white pubescent; corolla tubular-salverform, yellow to white, glabrous, the tube straight and angular, ca. 4 mm long, the lobes narrowly-triangular, ca. 1.5 mm long, erect; stamens inserted ca. midway on the corolla tube, the anthers ca. 0.8–1 mm long; ovary somewhat compressed, the stigma capitate. *Follicles* compressed, oval, woody, brown-tomentose, to 13 cm long and

10 cm wide; seeds numerous, the wing large and concentric, ca. 9–10 cm wide. Mexico, most of Central America, Colombia, Venezuela, and Guyana.

CANAL ZONE: Barro Colorado Island, *Croat 8159, 8504, Knight s.n.* (all MO). Fort Gulick, *Johnston 1747, Tyson & Keenan 3880* (both MO).

The Panamanian collections were in fruiting stages only, and the description was completed using Guatemalan material (*Cook & Doyle 47*, US) determined by Woodson.

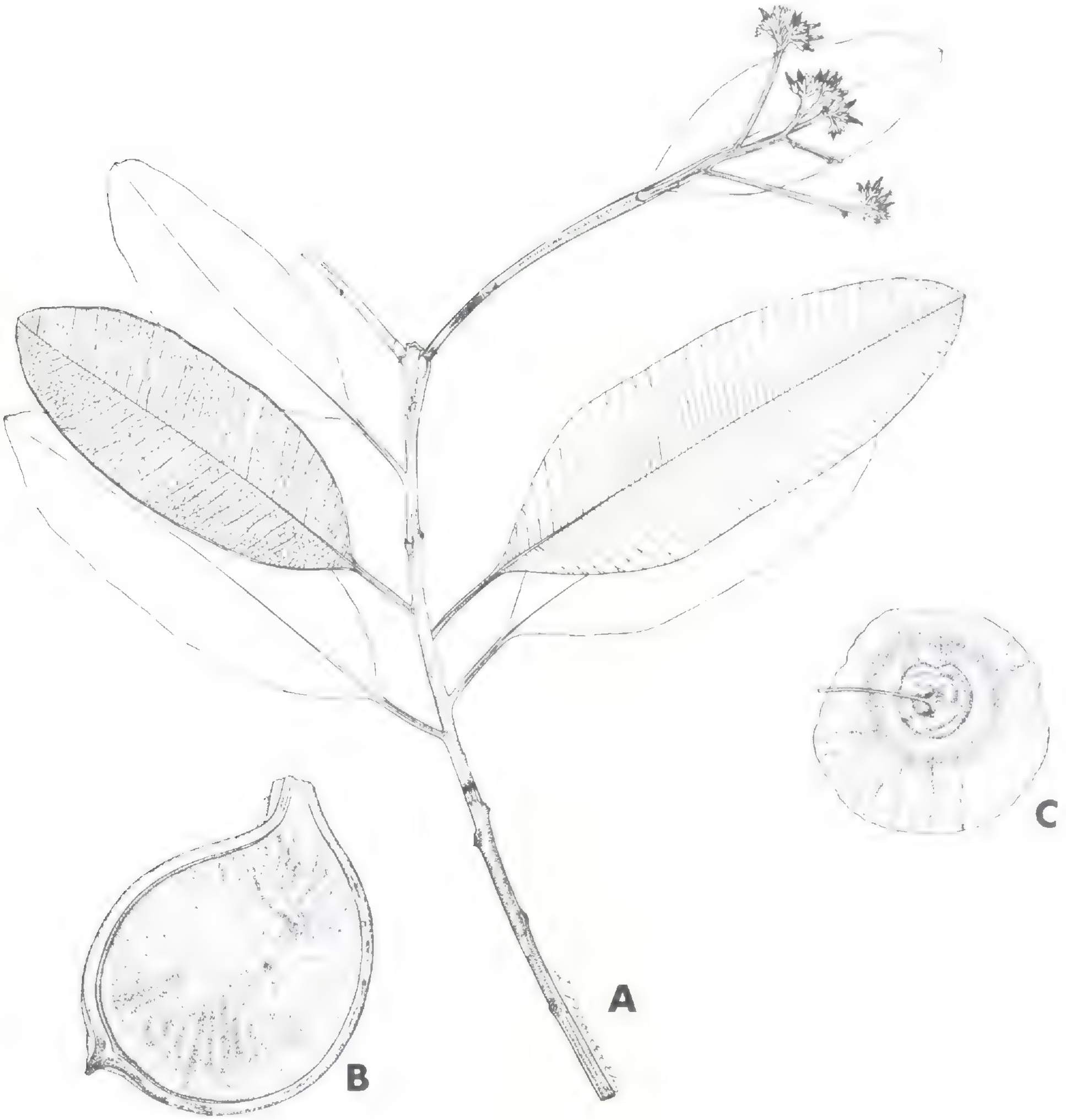

FIGURE 8. *Aspidosperma megalocarpon* Müll.-Arg.—A. Habit with inflorescence (× 3/5).—B. Fruit in longitudinal section (× 3/10).—C. Seed (× 3/10). [A, after *Cook & Doyle 47* (US); B, after *Johnston 1747* (MO); C, after *Tyson & Keenan 3880* (MO).]

2. **Aspidosperma darienense** Woodson *ex* Dwyer, Ann. Missouri Bot. Gard. 53: 104. 1966.

Trees, ca. 3–10 m high, juvenile branches with indistinct tufts of dirty-appearing hairs, soon glabrate, the bark brown, firm and striated, not lenticellate. *Leaves* irregularly decussate, subcaudate-acuminate, obtuse with uneven sides basally, 10–18 cm long and 2.5–5.5 cm wide, glabrous and shiny olive green above, pale and indistinctly papillate below, the secondary veins congested and widely ascending. *Inflorescences* lateral, extra axillary, with uneven sides, 2 to 3 times dichotomous, entirely minutely ferrugineous-puberulent, the peduncles moderately thick and subequal to the length of the petioles. *Flowers* in sessile fascicles, the bracts reniform, densely imbricate, ca. 1 mm long or less; calyx-lobes closely imbricate, subequal, suborbicular-reniform, obtuse, ca. 1–1.5 mm long, with minute, appressed ferrugineous hairs, ciliate, non-glandular; corolla apparently tubuliform to tubuliform-salverform, fleshy, minutely sericeous externally, the tube ca. 1.5 mm long, widely subcampanulate and not constricted, the lobes narrowly sagittate, not twisted in bud, ca. 1 mm long; anthers inserted at the base of the corolla tube in bud; ovary ca. 1.5 mm long, style ca. equal, minutely puberulent. *Fruit* unknown.

Known only from the type collection.

DARIEN: Lowland forest, between Río Chucunaque & Río Canglon, *Sexton & Knight s.n.* (MO, holotype).

The holotype collection has apparently been misplaced, and the description above is a translation of the Latin diagnosis.

One collection of *Aspidosperma* remains unnamed—Colón: Santa Rita lumber road, *Dressler 3440* (MO). The flowers of this collection are almost identical with those described for *A. darienense,* although the callose-angulate condition of the corolla is difficult to assess; the leaves, while irregularly decussate like those of *A. darienense,* a condition which is uncommon in the genus, are much smaller, ca. 5–7 cm long with bluntly acute apices and equal-sided bases. The genus is a large one, containing about 50 species, and Woodson's key to the series is based in part on fruit and seed characters. In view of the above restrictions, I think it advisable to wait for further collections or recovery of the holotype of *A. darienense* for purposes of comparison before describing a new species.

8. TONDUZIA

Tonduzia Pittier, Contr. U. S. Natl. Herb. 12: 103. 1908.

Shrubs, or small trees, lacticiferous (?). *Leaves* ternate or quadrate, rarely opposite, non-glandular, pinnately-nerved; petiolate, estipulate, sometimes glandular in the axils. *Inflorescences* thyrsiform, axillary or sub-terminal, many-flowered. *Flowers* small; calyx 5-lobed, the lobes ± equal, slightly imbricate, without squamellae within; corolla salverform, without appendages, the tube straight, the limb 5-lobed, the lobes sinistrorsely convolute; stamens 5, included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovules numer-

ous, the nectary low and annular or absent, the style 1, the stigma capitate above and somewhat umbraculiform below. *Fruit* apocarpous, of 2 follicles, terete; seeds numerous, compressed, dry, pubescent marginally.

A genus of three species in Mexico and most of Central America.

Tonduzia longifolia (A. DC.) Markgraf, Repert. Spec. Nov. Regni Veg. 20: 112. 1924.—FIG. 9.

Rauwolfia longifolia A. DC., Prodr. 8: 338. 1844.

Shrubs, or small trees, 3–6(–15) m, mostly glabrous. *Leaves* ternate or quadrate, oblong-elliptic, gradually acuminate, obtuse to attenuate basally, to 17 cm long and 2.5 cm wide, subcoriaceous, glabrous, the secondary veins obscure; petioles 5–15 mm long, glandular in the axils. *Inflorescences* thyrsiform, much smaller than the subtending leaves, congested. *Flowers* with the pedicels 2–4 mm long; bracteoles 2–3, ovate and keeled, ca. 1 mm long; calyx-lobes ovate-deltoid, 1–1.5 mm long; corolla white, the tube ca. 6–7 mm long, slightly expanded at the level of stamen attachment, pubescent within near the orifice and at the level of stamen attachment, the lobes obliquely oblong-obovate, ca. 3–4 mm long; stamens attached ca. midway on the corolla tube, the anthers ca. 1.2 mm long; nectary low and annular. *Follicles* 7–12 cm long.

Southern Mexico and most of Central America.

CHIRIQUI: Chiriquicito-Caldera Trail, between Pinola and Quebrada Seco, *Kirkbride & Duke 1031* (MO).

Due to the paucity of Panamanian material, the above description is based on a Mexican collection (*Hinton 3968*, MO) and Woodson's characterization of the species (N. Amer. Fl. 29: 122. 1938).

9. LOCHNERA

Lochnera Reichenb., Consp. Regni Veg. 134. 1828.

Catharanthus G. Don, Gen. Syst. 4: 95. 1837 (1838).

Herbs, annual or perennial, subsucculent or sometimes subshrubs, laciciferous. *Leaves* opposite, non-glandular, pinnately-nerved, sometimes slightly succulent; petiolate, glandular in the axils. *Inflorescences* cymose, sessile, sometimes reduced to a single flower, axillary. *Flowers* medium-sized; calyx 5-lobed, the lobes ± equal, without squamellae; corolla salverform, white to pink, without appendages, but the tube sometimes thickened near the orifice, the limb 5-lobed, sinistrorsely convolute; stamens 5, barely included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectaries 2, as high as the carpels and alternate with them, the style 1, the stigma pentagonal-umbraculiform. *Fruit* apocarpous, of 2 terete follicles; seeds numerous, dry, subcompressed, naked.

A genus of six species, four endemic to Madagascar, one to India, and one pantropical.

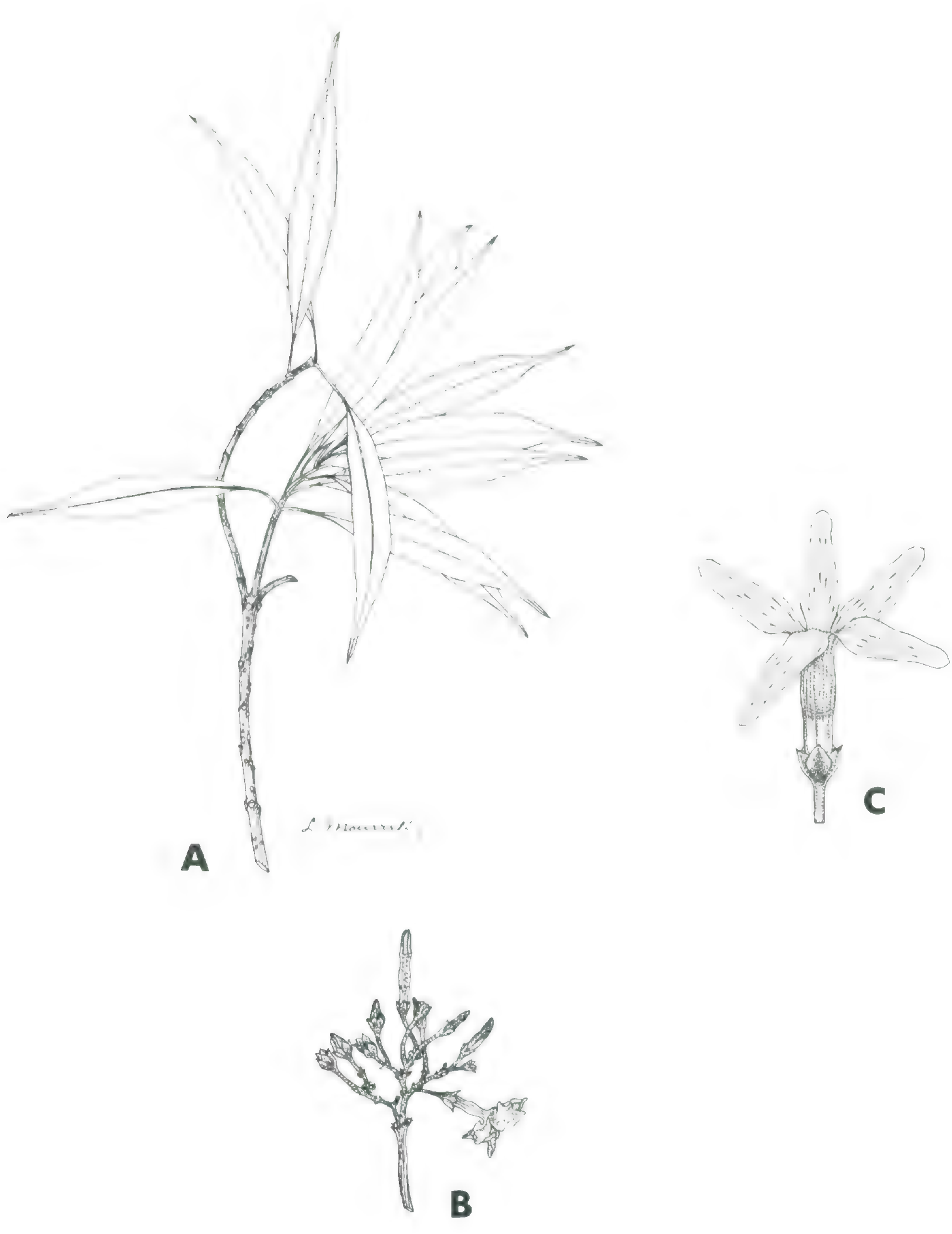

FIGURE 9. *Tonduzia longifolia* (A. DC.) Markgraf.—A. Habit (× 3/5).—B. Inflorescence (× 1 4/5).—C. Flower (× 2 2/5). [A, after *Kirbride & Duke 1031* (MO); B–C, after *Hinton 3968*, Mexico (MO).]

There is some disagreement concerning the validity of the generic name, *Lochnera* Reichenb., as opposed to *Catharanthus* G. Don. I follow Dwyer (Lloydia 27: 282–285. 1964) in using *Lochnera,* but admit that due to Reichenbach's (Consp. Regni Veg. 134. 1828) indirect reference to a previously published description, the choice is a tenuous one.

Lochnera rosea (L.) Reichenb., Consp. Regni Veg. 134. 1828.– FIG. 10A.

Vinca rosea L., Syst. Nat. ed. 10. 944. 1759.
Catharanthus roseus G. Don, Gen. Syst. 4: 95. 1837 (1838).

Herbs, suffrutescent basally, to 60 cm, the younger stems sparsely pubescent, lacticiferous. *Leaves* oblong-elliptic to ± spatulate, mucronulate, obtuse to attenuate basally, to 6 cm long and 3 cm wide, sparsely pubescent, more so on the veins beneath, rarely ± glabrous, slightly succulent; petioles 3–10 mm long, bearing several glands in the axils. *Inflorescences* cymose, sessile, 1–4-flowered, axillary and opposite. *Flowers* with the pedicels 1–3 mm long; calyx-lobes elongate-deltoid, ca. 5–7 mm long, sparsely pubescent; corolla salverform, white, lavender, or rose-pink, the tube 20–25 mm long, sparsely pubescent externally, densely so internally near the level of stamen attachment and the orifice, the lobes obovate-dolabriform, ca. 15–23 mm long, spreading; stamens included, attached near the apex of the corolla tube, the anthers ca. 2 mm long; ovary pubescent, the nectaries 2, 2–3 mm long at anthesis, the stigma pentagonal-umbraculiform. *Follicles* 2, slender, terete and longitudinally ridged, 15–25 mm long; mature seeds unknown.

Native to Madagascar, but widely cultivated and escaped in the tropics and subtropics.

CANAL ZONE: Barro Colorado Island, *Ebinger 204* (MO). Near Fort Randolph, *Standley 28758* (US). Río Pedro Miguel, near East Paraíso, *Standley 30011* (US). HERRERA: 4 mi. S of Los Pozos, *Tyson 2642* (MO).

10. VINCA

Vinca L., Sp. Pl. 209. 1753.

Herbs, perennial, erect or trailing, lacticiferous. *Leaves* opposite, non-glandular. *Inflorescences* 1-flowered, axillary, and alternate. *Flowers* medium-sized; calyx 5-lobed, the lobes ± equal, without squamellae; corolla infundibuliform, blue, rarely white, without appendages, the limb 5-lobed, sinistrorsely convolute; stamens 5, the anthers not connivent, with an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectaries 2, alternate with the carpels and about as large. *Fruit* apocarpous, of 2 follicles, terete; seeds numerous, dry, naked.

A genus of six species in Europe, Asia, and North Africa.

Vinca minor L. is cultivated in Panama and probably escaped, but no collections of it have been seen.

11. ANECHITES

Anechites Griseb., Fl. Brit. W. Ind. Is. 410. 1861.

Lianas, mostly slender. *Leaves* opposite, non-glandular, ± pubescent above, the hairs with hardened multicellular bases; petiolate, glandular in the axils. *Inflorescences* racemose, axillary and alternate. *Flowers* small to medium-sized; calyx 5-lobed, the lobes essentially equal, imbricate, bearing squamellae within; corolla salverform, white, without appendages, the limb 5-lobed, the lobes sinistrorsely convolute; stamens 5, wholly included, the anthers free and not agglutinated to the stigma; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules 4–12, the nectary annular, the style 1. *Fruit* apocarpous, follicular; seed 1 by abortion, dry, naked.

A monotypic genus in the West Indies, Panama, Colombia, and Ecuador.

Anechites nerium (Aubl.) Urban, Repert. Spec. Nov. Regni Veg. 16: 150. 1919.—FIG. 11.

Apocynum nerium Aubl., Hist. Pl. Gui. Fr. 1:277. 1775.

Lianas, slender, the stems sparsely pubescent. *Leaves* ± elliptic, acute-acuminate, obtuse to rounded basally, to 12 cm long and 6 cm wide, chartaceous, pubescent, the hairs on the upper surface stiff and with multicellular bases, softly pubescent at least on the midrib beneath; petioles to 3 cm long, glandular in the axils. *Inflorescences* racemose, few- to several-flowered, axillary, the peduncles ca. 9–12 cm long. *Flowers* with the pedicels ca. 5–15 mm long; calyx-lobes ovate-deltoid, ca. 1.5 mm long; corolla sparsely and softly pubescent externally, the tube ca. 4 mm long, pubescent within and slightly expanded at the level of stamen attachment, the lobes obliquely obovate, ca. 6–7 mm long; stamens attached near the middle of the corolla tube, the anthers ca. 0.8 mm long. "Follicles narrowly terete, 1-seeded by abortion, prolonged into a tapering sterile beak with ferruginous barbate hairs."[5]

Parts of the West Indies, Panama, Colombia, and Ecuador.

BOCAS DEL TORO: Changuinola Valley, *Dunlap* 589 (F, US). Vicinity of Chiriquí Lagoon, Pumpkin River, *von Wedel* 2570 (US); Garay Creek, *von Wedel* 2628 (MO, US); Water Valley, *von Wedel* 755 (US).

The characteristic pubescence, stiff hairs with multicellular bases, and the one-seeded follicular fruits make *Anechites nerium* distinctive among the Panamanian Apocynaceae.

12. THEVETIA

Thevetia Adans., Fam. Pl. 2: 171. 1763.

Plumeriopsis Rusby & Woodson, Ann. Missouri Bot. Gard. 27: 11. 1937.

Trees, shrubs or rarely lianas, lacticiferous. *Leaves* spiral, non-glandular, pinnately-nerved, frequently coriaceous and lustrous; sessile to petiolate, mostly

[5]In the absence of fruiting material a direct quote was taken from Woodson, N. Amer. Fl. 29: 141. 1938.

with intrapetiolar glands. *Inflorescences* cymose to racemose, axillary or terminal, few- to several-flowered. *Flowers* medium-sized to large, frequently showy; bracteoles present; calyx 5-lobed, the lobes ± equal, bearing many squamellae within; corolla salverform to infundibuliform, white, cream, orange, or pinkish-yellow, the orifice closed by 5 appendages, the limb 5-lobed, sinistrorsely convolute; stamens 5, wholly included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules 2–4, the nectary annular, the style 1, the stigma umbraculi-

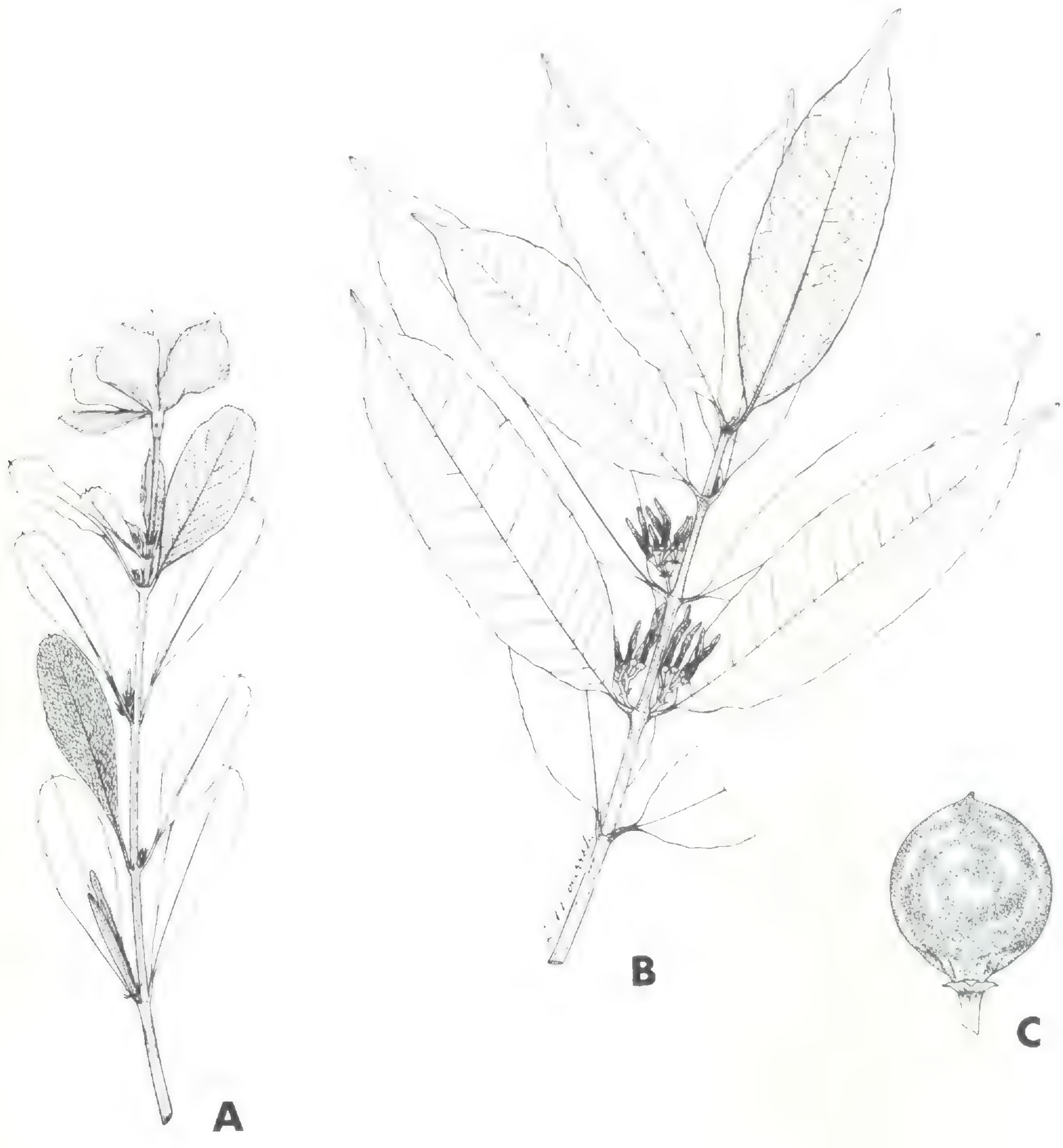

FIGURE 10. *Lochnera* and *Lacmellea*.—A. *Lochnera rosea* (L.) Reichenb., habit (× 3/5). [After *Ebinger 204* (MO.).]—B–C. *Lacmellea panamensis* (Woodson) Markgraf. —B. Habit (× ½).—C. Fruit (× 9/10). [B, after *Zetek 3818* (MO); C, after *Croat 5534* (MO.]

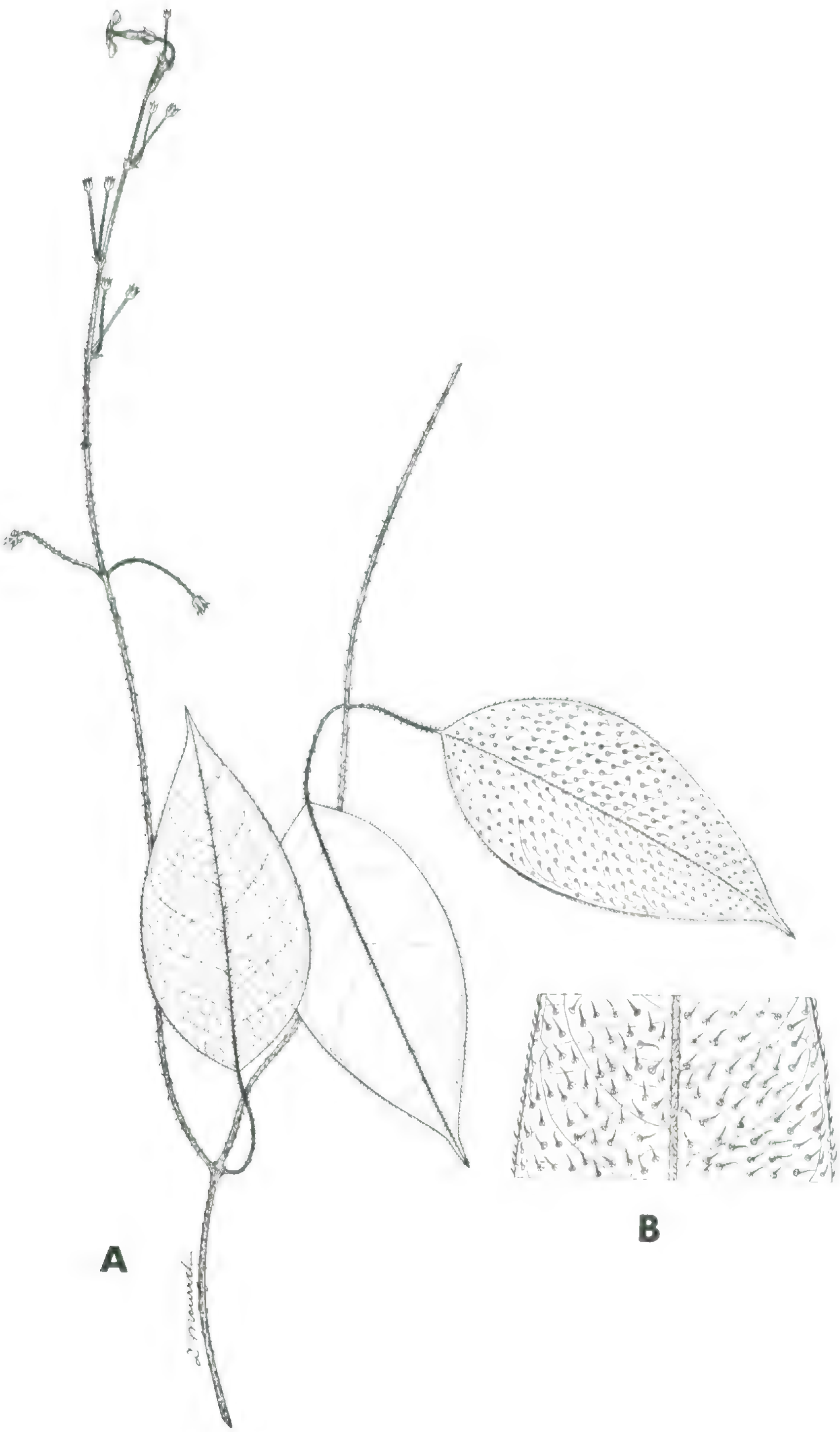

FIGURE 11. *Anechites nerium* (Aubl.) Urban.—A. Flowering branch (× 7/8).—B. Surface of leaf (× 2 1/10). [After *Dunlap* 589 (US).]

form below and bifid above. *Fruit* syncarpous, drupaceous, or berry-like, the pericarp coriaceous; seeds 2–4, ovoid, naked.

A genus of about six species in tropical America; frequently cultivated because of the handsome flowers.

The two species found in Panama had been placed in separate genera by Woodson (N. Amer. Fl. 29: 131–133. 1938), but I do not recognize *Plumeriopsis*.

a. Leaves narrowly-lanceolate, mostly < 1 cm wide, crowded . . . . . 1. *T. peruviana*
aa. Leaves ± obovate, at least some > 5 cm wide, not crowded . . . . . 2. *T. ahouai*

1. **Thevetia peruviana** (Pers.) K. Schum. *in* Engler & Prantl, Nat. Pfl. 4(2): 159. 1895.—Fig. 12.

Cerbera peruviana Pers., Syn. Pl. 1: 267. 1805.

Small *trees* or shrubs, to 7 m, the stems glabrous and somewhat corky. *Leaves* linear-lanceolate, acute, attenuate basally, to 15 cm long and 1 cm wide, glabrous, lustrous above, ± coriaceous, the secondary veins obscure; subsessile,

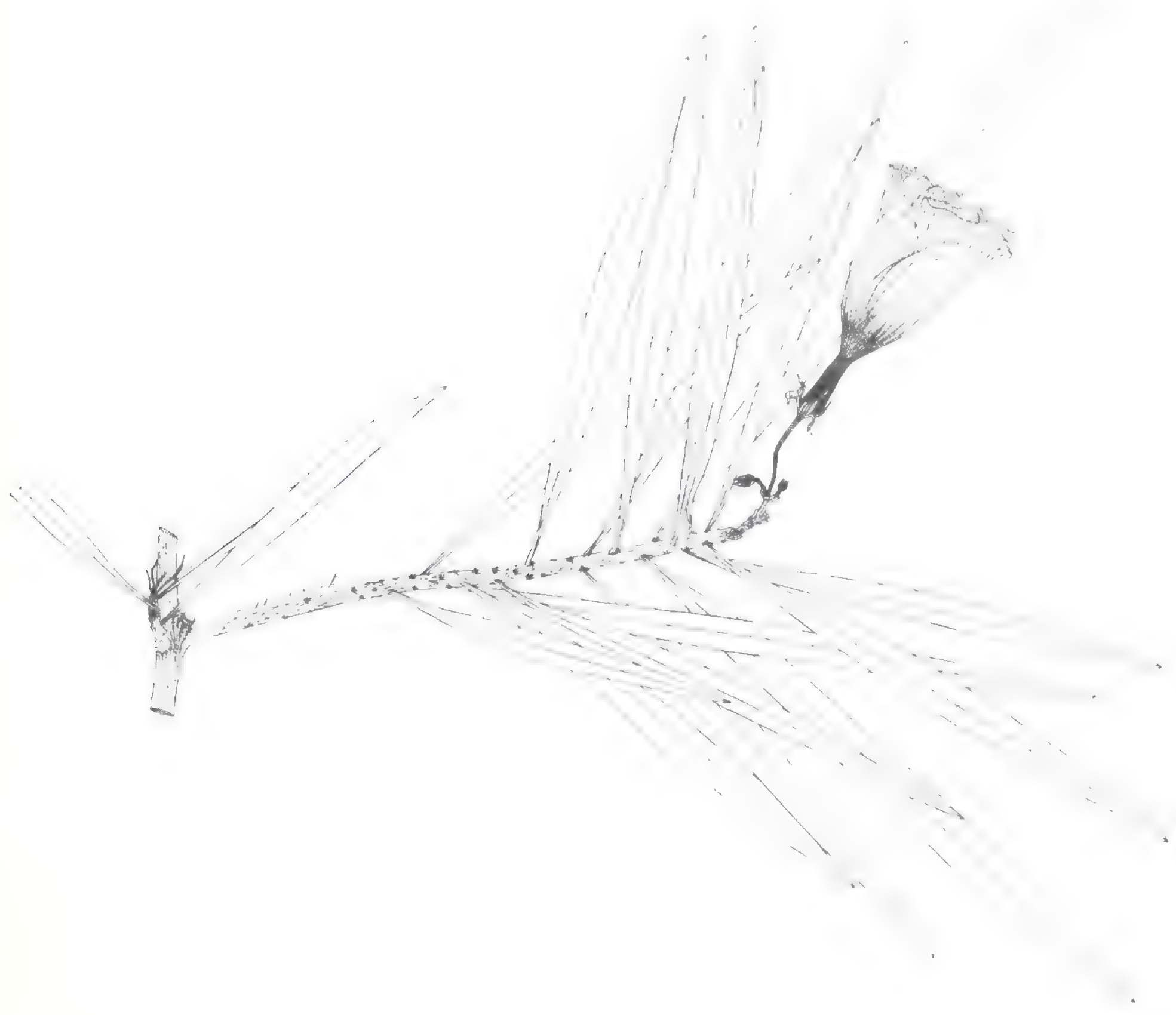

Figure 12. *Thevetia peruviana* (Pers.) K. Schum., general habit with flower (× ½). [After *Bro. Paul* 309 (US).]

bearing several glands in the axils. *Inflorescence*s cymose, mostly terminal, few-flowered, the peduncle short, < 1 cm long, the bracts elongate-deltoid, caducous. *Flowers* with pedicels to 3.5 cm long in fruit; bracteoles elongate-deltoid, 1.8–2 mm long, with several glands in the axil; calyx-lobes elongate-deltoid, ca. 5.5–7 mm long, glabrous, bearing several thin squamellae within basally; corolla infundibuliform, yellow, the tube proper ca. 12–15 mm long, pubescent near the throat and closed by 5 pubescent appendages, attached above and opposite the stamens, the throat ca. 15–18 mm long, the lobes ± erect, obovate-dolabriform, 30–35 mm long and to 17 mm wide; stamens included, attached at the apex of the tube proper, the anthers ca. 1.8 mm long, apically capped; ovary apocarpous, surrounded by an annular nectary, the stigma umbraculiform. *"Drupes"* weakly rhomboid, compressed, red, 2.5 cm high and 4 cm at the widest point; seeds 2(–4), naked, to 1 cm long.

Throughout tropical America; frequently cultivated.

CANAL ZONE: Ancón, Hospital grounds, *Pittier 3415* (US). COCLE: 1–5 mi. S on old road to coast, *Tyson & Blum 2582* (MO). COLON: Plaza, *Rose 22079* (US). PANAMA: Sabanas, *Bro. Paul 309* (US).

The crowded, narrowly lanceolate leaves and large showy flowers make this species very distinctive among the Panamanian Apocynaceae.

2. **Thevetia ahouai** (L.) A. DC., Prodr. 8: 345. 1844.—FIG. 13.

Cerbera ahouai L., Sp. Pl. ed. 2. 303. 1762.
Plumeriopsis ahouai (L.) Rusby & Woodson, Ann. Missouri Bot. Gard. 24: 11. 1937.
Ahouai nitida (H.B.K.) M. Pichon, Notul. Syst. (Paris) 13:227. 1948.

Trees or shrubs, to 8 m, the stems ± glabrous. *Leaves* oblong-obovate, acute-acuminate, obtuse to attenuate basally, to 30 cm long and 8 cm wide, glabrous on both surfaces to minutely puberulent beneath, coriaceous, the secondary veins anastomozing to form a marginal vein; subsessile to petioles ca. 1 cm long, bearing several glands in the axil. *Inflorescences* cymose, irregular, mostly terminal, the peduncle indistinct, the bracts not apparent. *Flowers* with the pedicels to 3 cm long at maturity; bracteoles broadly ovate, ca. 2–4 mm long, caducous; calyx-lobes ovate, 5–7 mm long, somewhat reflexed, bearing numerous thin squamellae within; corolla ± salverform, cream-colored, the tube ca. 25–35 mm long, pubescent within, closed by 5 pubescent appendages attached above and opposite the stamens, the lobes obovate-dolabriform, ca. 15–20 mm long; stamens included, attached at the top of the corolla tube, the anthers ca. 2 mm long, elongate apically; ovary apocarpous, surrounded by an annular nectary, the stigma umbraculiform with a bifid apex. *"Drupes"* obreniform-obpyriform, red, 3.5–4 cm wide; seeds 2–4, naked, large.

Southern Mexico, Central America, and northern South America; common in Panama.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, Old Bank Island, *von Wedel 1899* (MO); Water Valley, *von Wedel 1593* (MO). CANAL ZONE: Barro Colorado Island, *Croat 5032, 5844, 8359, 8573, Ebinger 608, Oppenheimer 1145, Shattuck 162* (all MO). Vicinity of Cerro Viejo, *Blum 1232* (MO). Farfan Beach, *Duyer 6763, Lewis et al. 59, Tyson 1826, 1835, Tyson & Blum 2621, Tyson et al. 3163* (all MO). Vicinity of Fort Sherman, *Blum & Duyer 2104, Duyer 7200* (both MO). Road from Fort Sherman to Fort

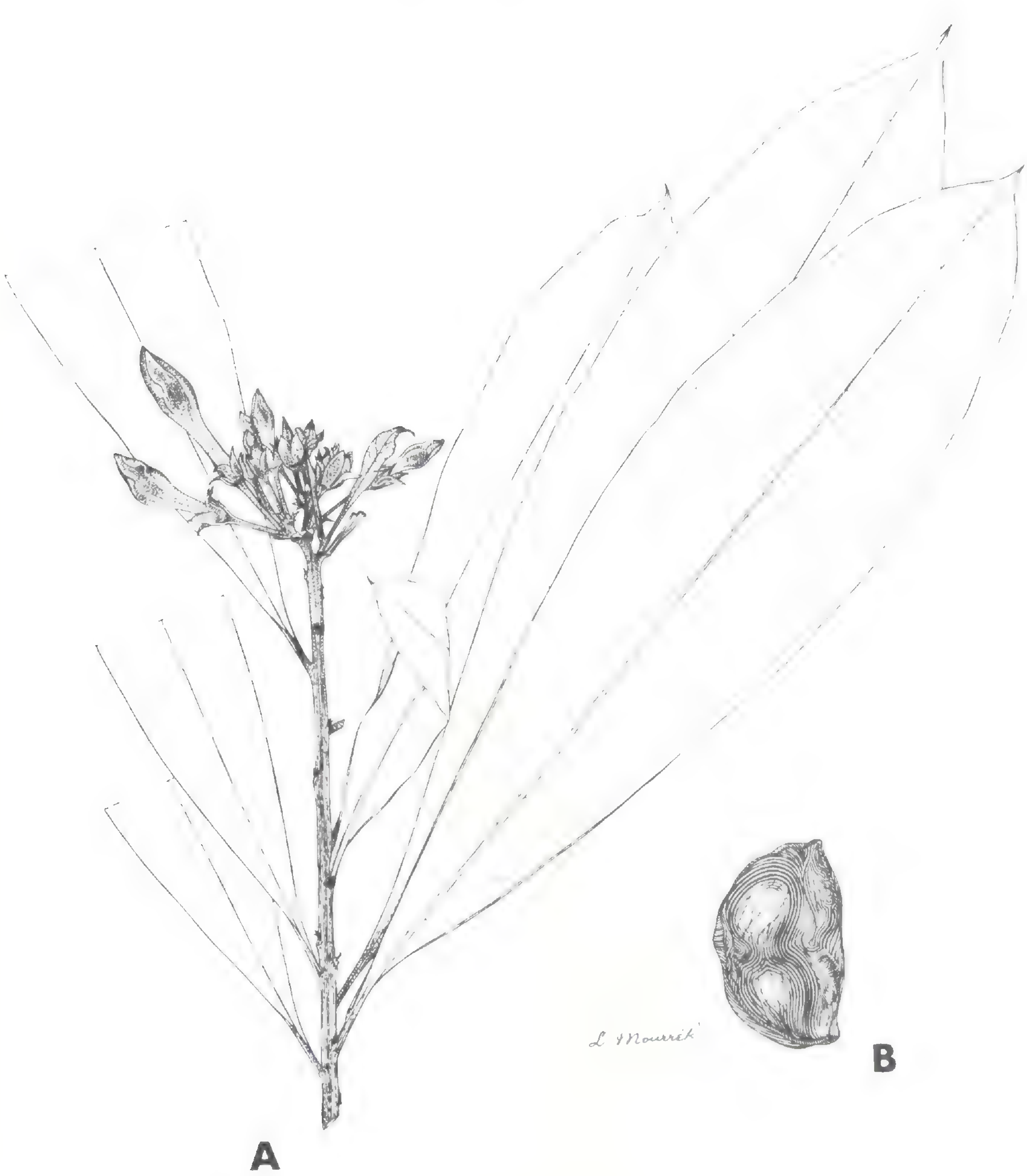

FIGURE 13. *Thevetia ahouai* (L.) A. DC.—A. Habit with immature inflorescence (× 3/5).—B. Fruit (× 3/5). [A, after *Tyson 1826* (MO); B, after *Lewis et al.* 5345 (MO).]

San Lorenzo, *Porter et al.* 4989 (MO). Fort Kobbe, *Duke* 3969 (MO). Madden Dam, *Dwyer & Robyns 127* (MO). Madden Forest Preserve, *Lewis et al.* 5345 (MO). 2 mi. N of Road K-10 on Pan American Highway, *Lewis et al.* 5230 (MO). Pipeline Road, 16 mi. N of Gamboa, *Lewis et al.* 5430 (MO). CHIRIQUI: Vicinity of Puerto Armuelles, *Woodson & Schery* 897 (MO). Vicinity of San Bartolomé, *Woodson & Schery* 916 (MO). DARIEN: Vicinity of Paya, Río Paya, *Stern et al. 371A* (MO). Along Quebrada Maskia off Río Pucro, above Pucro, *Duke 13102* (MO); Quebrada Barbua, trail ca. 2 km W, *Stern et al.* 98 (MO). Between Quebrada Venado & Peji Swamp on headwaters of Río Tuqueza, *Bristan 1047* (MO). Hill near Río Chucunaque, ca. 4 mi. below Yaviza, *Duke* 4868 (MO). HERRERA: Vicinity of Ocú, *Stern et al. 1744* (MO). 10 mi. S of Ocú, *Tyson et al. 2854* (MO). 12 mi. S of Ocú, *Lewis et al. 1667* (MO). LOS SANTOS: Vicinity of headwaters Río Pedregal, *Lewis et al.*

2921 (MO). Río Tonosí, vicinity of Tonosí, *Lewis et al. 1535* (MO). PANAMA: Thickets and forests near Arraíjan, *Woodson et al. 1350* (MO). Cerro Campana, *Lewis et al. 3146, Porter et al. 4316* (both MO). Tributary of Río Chagres, 5 mi. SW of Cerro Brewster, *Lewis et al. 3448* (MO). Taboga Island, *Woodson et al. 1524* (MO). Tocumen, *Dwyer 4352* (MO). SAN BLAS: Isla de Pinos, *Kirkbride 209* (MO).

13. RAUVOLFIA

Rauvolfia L., Sp. Pl. 208. 1753.

Shrubs or trees, rarely vine-like, lacticiferous, the branches usually whorled. *Leaves* whorled, (3–)4(–5), ± anisophyllous within a whorl, non-glandular along the midrib, pinnately nerved, membranaceous to coriaceous, sessile to petiolate, glandular in the axils, sometimes on the petiole; stipules small and deciduous. *Inflorescences* cymose, dichasial, terminal or axillary, few- to many-flowered. *Flowers* ± small; calyx 5-lobed, the lobes equal, without squamellae; corolla salverform, infundibuliform, urceolate, or campanulate, without appendages, the limb 5-lobed, sinistrorsely contorted; stamens 5, included, the filaments short, the anthers free and not agglutinated to the stigma; gynoecium 2-carpellate, apocarpous or syncarpous, the ovary superior, the ovules 2–4, the nectary annular or cupuliform, entire or dentate, the style 1, the stigma cylindrical, calyptriform or sub-mitriform, obscurely biapiculate. *Fruit* apocarpous or syncarpous, drupaceous; seeds 1–4, naked.

A large pantropical genus of about 110 species.

Three species are found in Panama: *Rauvolfia purpurascens* Standley, *R. littoralis* Rusby, and the common *R. tetraphylla* L. One other species, *R. ligustrina* Roem. & Schult., is conspicuously absent. According to Rao (p. 281) this species is in a section characterized by ternate leaves, of which the largest is 3–5 cm long, and inflorescences about as long as the largest associated leaf. Panamanian collections which correspond to this description have been assigned to *R. littoralis* because the calyces are totally unlike that pictured for *R. ligustrina* (Rao, p. 299, Fig. 8).

Useful reference:

Rao, A. S. A revision of *Rauvolfia* with particular reference to the American species. Ann. Missouri Bot. Gard. 43: 253–354. 1956.

a. Leaves with glands in the axils only; corolla salverform, the tube > 4 mm long ..... 1. *R. purpurascens*
aa. Leaves glandular on the petioles and in the axils; corolla urceolate, < 4 mm long.
  b. Leaves obovate, acuminate, gradually tapering basally; calyx-lobes obtuse or rounded ..... 2. *R. littoralis*
  bb. Leaves ovate to ovate-elliptic, acute, abruptly tapering basally; calyx-lobes acute ..... 3. *R. tetraphylla*

1. **Rauvolfia purpurascens** Standley, Trop. Woods 16: 11. 1928.

Lianas (?), the stems glabrous. *Leaves* mostly ternate, obovate, acute, obtuse basally, to 17 cm long and 7 cm wide, glabrous, slightly coriaceous; petioles non-glandular, ca. 1–2.5 cm long, glandular in the axils. *Inflorescences* cymose, paired, the peduncles 4–5.5 cm long. *Flowers* with the pedicels ca. 3–5 mm long; bracteoles minute, ca. 0.1–0.2 mm long; calyx-lobes ovate, ca. 1–1.2 mm

long; corolla salverform, purple-tinted (*Cooper 516*), glabrous externally, the tube ca. 6–7 mm long, pubescent near the level of stamen attachment, the lobes ± obovate, ca. 4–5 mm long; stamens attached near the top of the corolla tube, the anthers ca. 0.8 mm long; ovary ± syncarpous, the nectary cupulate, the ovules 2, the stigma columnar. *Fruit* unknown.

Known only from the type collection.

BOCAS DEL TORO: Cricamola, *Cooper 516* (F, holotype).

2. **Rauvolfia littoralis** Rusby, Descr. New Sp. S. Amer. Pl. 84. 1920.—FIG. 14.

R. multiflora Riley, Kew Bull. 1927: 124. 1927.
R. macrocarpa Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 254. 1929.

Shrubs or small trees, to 10 m, glabrous to softly pubescent on the younger branches. *Leaves* quarternate or ternate, distinctly anisophyllous, obovate, rarely

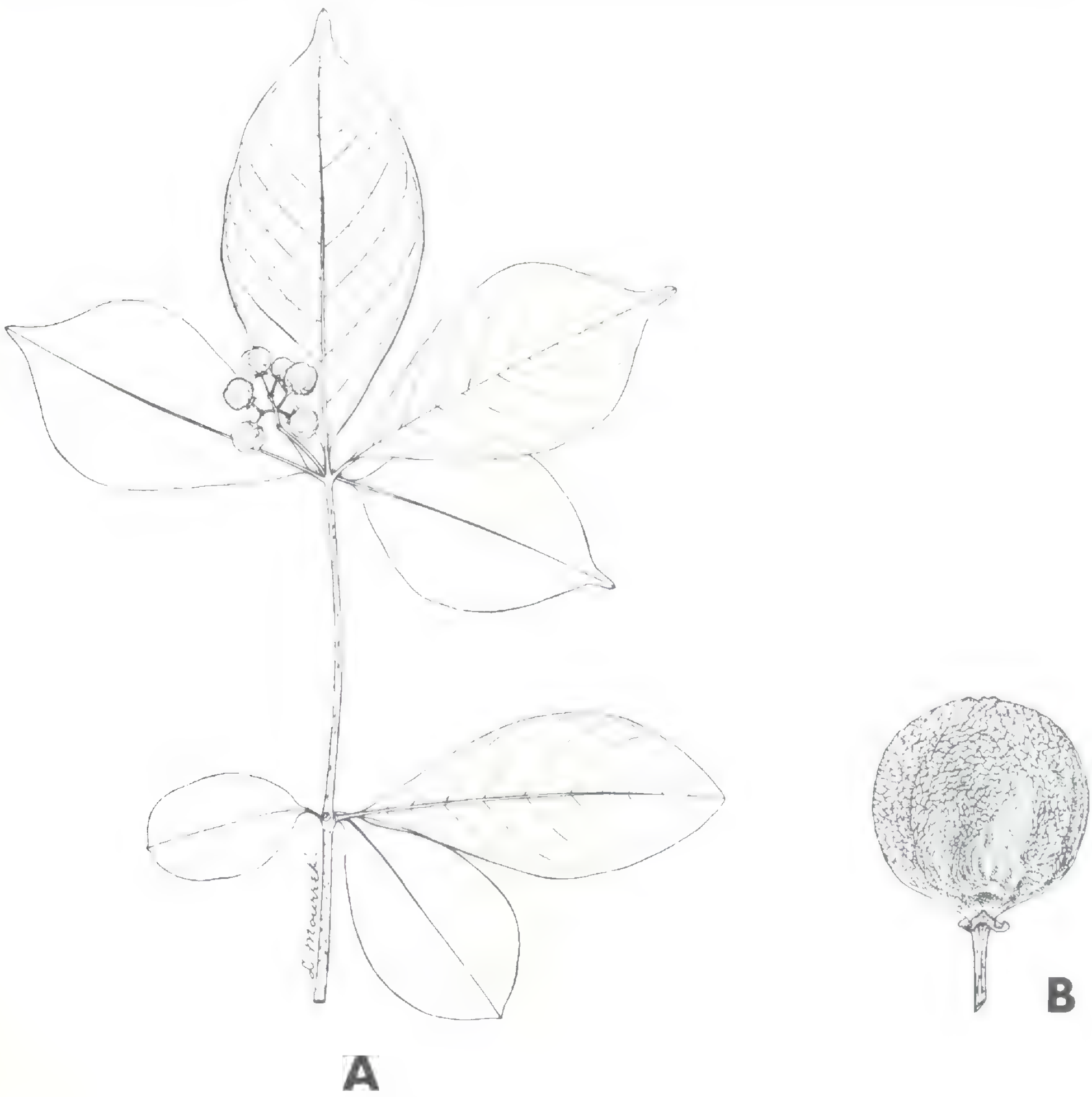

FIGURE 14. *Rauvolfia littoralis* Rusby.—A. Habit (× ½).—B. Fruit (× 2 4/5). [After *Dwyer 6726* (MO).]

elliptic or broadly ovate, acute to acuminate, obtuse basally, the larger leaves to 14 cm long and 6 cm wide, the smaller leaves ¼ to ½ the size of the larger, glabrous to sparsely pubescent on the midrib above and beneath, firmly membranaceous; petioles glandular, ca. 2–6 mm long, glandular in the axils. *Inflorescences* cymose, axillary and opposite, the peduncle 1–4 cm long, softly pubescent to ± glabrous, bracts minute. *Flowers* with the pedicels ca. 2–5 mm long; calyx-lobes broadly ovate and rounded, the margin frequently fimbriolate, ca. 0.6–0.8 mm long; corolla broadly tubular, white, the tube ca. 2–2.5 cm long, pubescent within, the lobes ± deltoid, erect, ca. 0.4 mm long; stamens attached near the top of the corolla tube, the anthers ca. 0.5 mm long; ovary syncarpous, the nectary cupulate, shallow, and entire, the stigma depressed-capitate. *Drupes* ± spherical, ca. 6–8(–15) mm in diameter, becoming dark-red to black at maturity, the bony endocarp rugose; seeds 2, ovoid.

Costa Rica, Panama, Colombia, and Ecuador.

CANAL ZONE: Albrook Tower, vicinity of Tropic Test Center, *Blum 552, Dwyer 6726* (both MO). Farfan Spillway, *Bouche s.n.* (MO). Fort Kobbe Beach, *Bouche s.n.* (MO). Near Gorgas Memorial Lab, *P. White 120* (MO). Vicinity of Miraflores Lake, *White 137* (MO). CHIRIQUI: Progreso, *Cooper & Slater 200* (US, isotype of *R. macrocarpa*). DARIEN: Hill near Río Chucunaque ca. 4 mi. below Yaviza, *Duke 4876* (MO). Cuipo forests near Santa Fé, *Duke 12289* (MO). PANAMA: Cerro Campana, *Bartlett & Lasser 16919* (MO). Vicinity of Coccolí, *Riley 125* (MO, US, isotypes of *R. multiflora*). Tocumen, *Dwyer 1080* (MO).

3. **Rauvolfia tetraphylla** L., Sp. Pl. 208. 1753.—FIG. 15.

Shrubs, to ca. 2 m, or sometimes trees to ca. 4 m, the stems glabrous to softly pubescent. *Leaves* mostly quarternate, conspicuously anisophyllous, elliptic to ovate-elliptic, rarely weakly obovate, acute, obtuse to attenuate basally, the larger leaves to 17 cm long and 7 cm wide, the smaller leaves ca. ½ as long as the largest, glabrous to occasionally sparsely pubescent on both surfaces; petioles glandular, ca. 1–7 mm long, glandular in the axils. *Inflorescences* cymose, axillary or terminal, few-flowered, the peduncle ca. 1–4 cm long, sometimes sparsely pubescent. *Flowers* with the pedicels ca. 3–5 mm long; calyx lobes ovate, ± acute, ca. 1.5 mm long, the margin frequently fimbriolate; corolla urceolate, white, glabrous or pubescent externally, the tube ca. 2–3 mm long, pubescent within near the orifice, the lobes shallow and rounded, erect, ca. 1 mm long; stamens attached near the top of the corolla tube, the anthers ca. 0.8 mm long; ovary syncarpous, the nectary cupulate, entire, the stigma subcapitate. *Drupes* ± spherical and bilobed, ca. 5–8 mm in diameter, red, becoming black with maturity, the bony endocarp distinctly rugose; seeds 2, ovoid.

Mexico, Central America, the West Indies, northern South America, and introduced and naturalized in India and Australia.

CANAL ZONE: Ancón, *Bouche s.n.* (MO). COCLE: El Valle de Antón, *Duke & Dwyer 13895, Lewis et al. 2618* (both MO). DARIEN: Vicinity of El Real, Río Tuira, *Stern et al. 113, 757* (both MO). LOS SANTOS: Monagre Beach, *Burch et al. 1206, Lewis et al. 1674, Tyson et al. 3007* (all MO). Río Tonosí, vicinity of Tonosí, *Lewis et al. 1565* (MO). PANAMA: Sabanas N of Panama City, *Bro. Paul 446* (MO). Old Panama City, *Greenman & Greenman 4145* (MO). Along beach from Panamá Viejo to Bella Vista, *Allen 831* (MO). Taboga Island, *Woodson et al. 1530* (MO). Vera Cruz, *Lewis et al. 2999* (MO).

Rauvolfia tetraphylla is a wide ranging and variable species. The characters which separate it from *R. littoralis* Rusby, *i.e.*, leaf shape and apex, and sepal tip, overlap. While many collections can be readily identified, there are specimens which have characteristics of both and are impossible to classify.

14. LACMELLEA

Lacmellea Karst., Linnaea 28: 450. 1857.

Zschokkea Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 20. 1860.

Trees or shrubs, lacticiferous, the stems with or without spines. *Leaves* opposite, non-glandular, pinnately-nerved; shortly petiolate, ± glandular in the axils. *Inflorescences* corymbose or cymose, axillary, opposite or alternate, mostly few-flowered, the peduncle short. *Flowers* small to medium-sized; calyx 5-lobed, the lobes ± equal, mostly without squamellae; corolla salverform, without append-

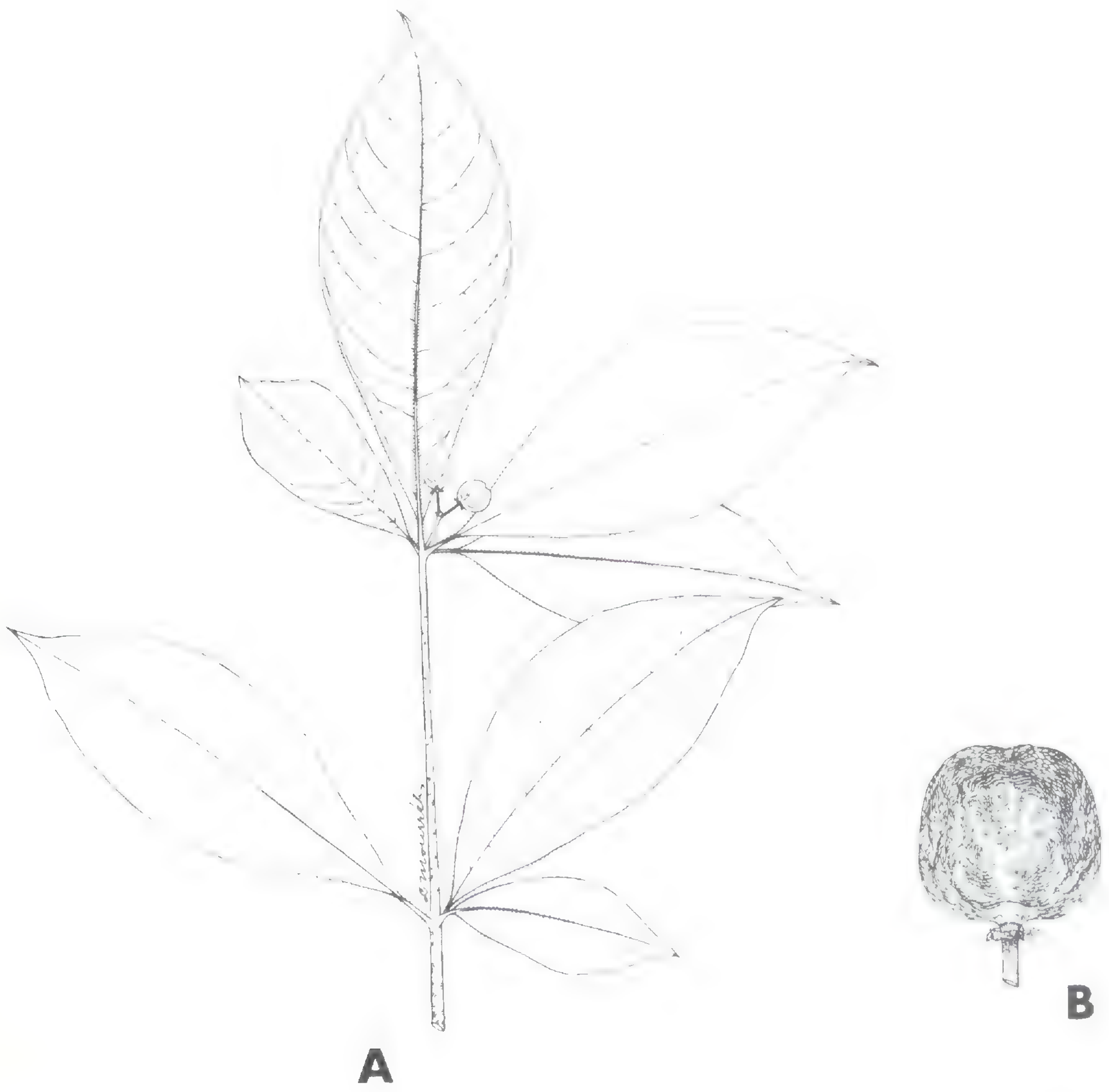

FIGURE 15. *Rauvolfia tetraphylla* L.—A. Habit (× 7/10).—B. Fruit (× 2 4/5). [After *Lewis et al. 1565* (MO).]

ages, the tube slightly gibbous or straight, the limb 5-lobed, sinistrorsely convolute; stamens 5, included, the anthers free and not agglutinated with the stigma, without an enlarged connective; gynoecium 2-carpellate, syncarpous, the ovary superior, ovules several per locule, the nectary annular and ± adnate to the ovary, the style 1, not reaching the level of the anthers at anthesis, the stigma cylindrical, ± papillose. *Fruit* syncarpous, a small berry; seeds 1–4, ovoid, naked.

A genus of about 19 species found in northern South America; two species are found in Central America.

Markgraf (Notizbl. Bot. Gart. Berlin-Dahlem 15: 615–619. 1941) reduced *Zschokkea* to *Lacmellea* after concluding that the characters formerly maintaining their separation, *i.e.*, length of the style, level of the insertion of the anthers, and length of the corolla tube, were due simply to different stages of growth. Monachino (Lloydia 7: 275–302. 1944) also transferred *Zschokkea* to *Lacmellea*, apparently unaware of Markgraf's earlier reduction. Judging from his later annotation labels, Woodson also agreed with the congeneric status.

Lacmellea panamensis (Woodson) Markgraf, Notizbl. Bot. Gart. Berlin-Dahlem 15: 622. 1941.—FIG. 10B–C.

Zschokkea panamensis Woodson, Trop. Woods 44: 22. 1935.

Trees, to 20 m, the stems sometimes spiny, essentially glabrous. *Leaves* oblong-elliptic, acuminate, obtuse basally, to 12 cm long and 3.5 cm wide, coriaceous, glabrous; petioles ca. 0.5 cm long, weakly perfoliate, sparsely glandular in the axils. *Inflorescences* cymose, axillary, mostly opposite, 4–10 flowered, the peduncles ca. 4–6 mm long, the bracts deltoid, minute, ca. 1 mm long. *Flowers* with the pedicels ca. 2–4 mm long; bracteoles 2, deltoid, minute, ca. 1 mm long; calyx-lobes somewhat connate basally, broadly ovate, ca. 1–1.5 mm long, the margins minutely ciliate; corolla salverform, white, "the tube somewhat gibbous, 20–25 mm long, about 1.5 mm in diameter at the base, somewhat inflated at the insertion of the stamens, the lobes broadly and obliquely oblong-elliptic, 7–8 mm long, slightly spreading;"[6] stamens included, the anthers ca. 4 mm long; style not reaching the anthers at anthesis, the stigma cylindrical and papillose. *Berry* (?) ovoid-elliptic, ca. 2–3 cm long, orange-yellow; seeds 1–4, ellipsoid, dry, naked, ca. 1 cm long.

British Honduras and Panama.

CANAL ZONE: Barro Colorado Island, *Aviles 88* (F), *Croat 5035, 5166, 5373, 5534, 7676, 7678* (all MO), *Wilson 98*, *Woodworth & Vestal 470* (both F), *639* (F, holotype), *Zetek 3452* (F), *3818* (F, MO). NW part of Canal Zone, near Pavon Road, *Johnston 1780* (MO).

Spiny stems have not been previously attributed to *Lacmellea panamensis*, but the label of one collection [*Croat 7676* (MO)] states "trunk densely covered with spines." This collection appears similar in all other characters to the Panamanian material, although it is in fruit rather than in flower, as are the others.

[6] In the absence of good flowering material, a direct quote was taken from Woodson's description, N. Amer. Fl. 29: 142. 1938.

15. ALLAMANDA

Allamanda L., Mant. Pl. Altera 214. 1771.

Shrubs, sometimes subherbaceous, erect or lianoid, lacticiferous. *Leaves* quaternate or opposite, rarely alternate above, non-glandular, pinnately-nerved; petiolate, glandular in the axils. *Inflorescences* cymose, few- to several-flowered, axillary or (falsely ?) terminal. *Flowers* large and showy; calyx 5-lobed, the lobes ± equal, foliaceous, without squamellae within; corolla infundibuliform, without appendages, the limb 5-lobed, sinistrorsely convolute; stamens 5, included, the anthers free and not agglutinated to the stigma, without an enlarged connective; gynoecium 2-carpellate, syncarpous, the ovary superior, the ovules numerous, the nectary annular, the style 1, the stigma umbraculiform below and bicapitate above. *Fruit* a capsule, globose or subglobose, spiny; seeds numerous, dry, compressed, concentrically winged.

A genus of about 18 species in the tropics of South America; one species is found in Central America.

Allamanda cathartica L., Mant. Pl. Altera 214. 1771.—FIG. 16.

Lianas, sometimes shrubs to ca. 2 m, glabrous or the younger stems ± pubescent. *Leaves* quaternate, rarely opposite or alternate above, mostly obovate, sometimes elliptic, shortly acuminate, obtuse to attenuate basally, to 16 cm long and 6 cm wide, subcoriaceous, glabrous, or pubescent on the veins beneath, the secondary veins anastomosing and forming a marginal vein; subsessile to petioles 2–3 mm long. *Inflorescences* cymose, few-flowered, the peduncles ca. 1–4 cm long. *Flowers* with the pedicels ca. 2–7 mm long; bracteoles minute; calyx-lobes subequal, ovate to narrowly ovate, 5–12 mm long and 3–7 mm wide; corolla yellow, the tube proper ca. 20–35 mm long, pubescent at the level of stamen attachment, the throat broadly conic, ca. 20–35(–40) mm long, the lobes subequal, obliquely ovate, ca. 25–35 mm long and 30–45(–55) mm wide, spreading; stamens attached at the top of the tube proper, the anthers ca. 4 mm long; nectary shallow and annular. *Capsule* subglobose, ca. 2–3 cm in diameter, spinulose, the spines ca. 0.5–1 cm long; seeds 13–15 mm long.

Native to northeastern South America, but widely cultivated and escaped in the tropics of both hemispheres.

BOCAS DEL TORO: Almirante along the road to the "Bomba," *Blum 1347* (MO). Chiriquí Lagoon, Colón Island, *von Wedel 550* (MO); Fish Creek Hills, *von Wedel 2428* (MO); Water Valley, *von Wedel 1675* (MO). CANAL ZONE: Barro Colorado Island, *Croat 5921, 6567, 6573, 8109, Ebinger 599* (all MO). Vicinity of Contractors Hill, along Road K-2, *Lewis et al. 2878* (MO). Government forest along Las Cruces Trail, *Hunter & Allen 668* (MO). Río Chagres, *Fendler 457* (MO). CHIRIQUI: Vicinity of Tole, *Tyson et al. 4224* (MO). COLON: Nuevo Chagres, beach and adjacent roadside, *Lewis et al. 1861* (MO). DARIEN: Vicinity of Patino, *Duke 10529* (MO). Vicinity of El Real, Río Tuira, *Stern et al. 294* (MO, US). PANAMA: San José Island, along road between Bodega Bay & Río Mato Puerco, *Duke 12504* (MO).

The spiny capsule and the quaternate leaves make this species very distinctive. One collection, *Stern et al. 294* from Darién, is perplexing—the US specimen, a mid-branch portion, has quaternate leaves, and the MO specimen, a terminal

FIGURE 16. *Allamanda cathartica* L.—A. Habit with inflorescence (× ½).—B. Fruit (× 1/3).—C. Seed (× 1 1/10). [A, after *Lewis et al. 1861* (MO); B–C, after *Lewis et al. 2878* (MO).]

branch, has opposite and alternate leaves. Although I have seen many collections of this species which included terminal branches, only one other, *von Wedel 550* (MO), shows this alternate condition. However, a variation in leaf arrangement, such as opposite below and alternate above, can be found in other apocynaceous genera.

16. ALLOMARKGRAFIA

Allomarkgrafia Woodson, Ann. Missouri Bot. Gard. 19: 45. 1932.

Lianas, oppositely-branched below, becoming alternate above, lacticiferous. *Leaves* opposite, glandular at the base of the midrib, pinnately-nerved; petioles somewhat perfoliate, minutely glandular in the axils. *Inflorescences* racemose, bostrychoid, axillary and alternate. *Flowers* medium-sized, bracteolate; calyx 5-

lobed, the lobes subequal, bearing many squamellae within; corolla infundibuliform, without appendages, the tube proper straight, the limb 5-lobed, dextrorsely convolute; stamens 5, included, the anthers connivent and agglutinated to the stigma, with an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the style 1, the stigma ± umbraculiform-fusiform. *Fruit* apocarpous, of 2 terete follicles; seeds numerous, dry, comose apically.

A genus of about four species in Costa Rica, Panama, Colombia, and Peru.

Allomarkgrafia plumeriaeflora Woodson, Ann. Missouri Bot. Gard. 20: 627. 1933.—FIG. 17.

Lianas, glabrous, the stems terete or sometimes angular, the mature stems lenticular. *Leaves* oblong-elliptic, shortly acuminate to acute, sometimes mucronate, obtuse or slightly rounded basally, to 12 cm long and 5 cm wide, glabrous, coriaceous; petioles to ca. 1.2 cm long, stipules obsolete (?). *Inflorescences* racemose, the primary peduncle dichotomous or trichotomous, axillary and alternate, many-flowered. *Flowers* with the pedicels to 9 mm long; bracteoles 1, deltoid and somewhat keeled, ca. 2 mm long, regularly placed at the base of the pedicels, persistent, conspicuously so after the corolla and calyx are lost; calyx-lobes sub-equal, ovate and rounded, ca. 1.8–2.2 mm long, each bearing 2 groups of squamellae, alternately placed; corolla subinfundibuliform, pale yellow to white, the tube proper ca. 9–11 mm long, inflated near the base, the throat ca. 7 mm long, the lobes dolabriform, ca. 12–14 mm long; stamens ± included, the filaments short and pubescent, the anthers ca. 4 mm long; nectaries 5, slightly concrescent basally and somewhat lobed apically, at least as high as the ovary, the stigma umbraculiform below and ribbed and biapiculate above. *Follicles* unknown.

Costa Rica, Panama, and Colombia.

PANAMA: Cerro Campana, *Duke* 8653, *Lewis et al.* 3162 (both MO).

Because of the poor or immature condition of the Panamanian collections, the description was completed from Costa Rican material (*Skutch* 2323, US), determined by Woodson.

17. MESECHITES

Mesechites Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 150. 1860.

Echites of many authors, in part, not P. Br., Civ. Nat. Hist. Jamaica 181. 1756.

Lianas, sometimes ± herbaceous, lacticiferous. *Leaves* opposite, bearing 1–4 glands at the base of the midrib, pinnately-nerved; petioles somewhat perfoliate, mostly glandular in the axils. *Inflorescences* racemose, bostrychoid, axillary and alternate. *Flowers* mostly medium-sized; calyx 5-lobed, the lobes equal to sub-equal, bearing several alternate or irregularly placed squamellae within; corolla salverform, without appendages, the limb 5-lobed, the lobes dextrorsely convolute; stamens 5, included, the anthers connivent and agglutinated to the stigma, with an enlarged connective characterized by a pedestal-like projection; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectaries 5,

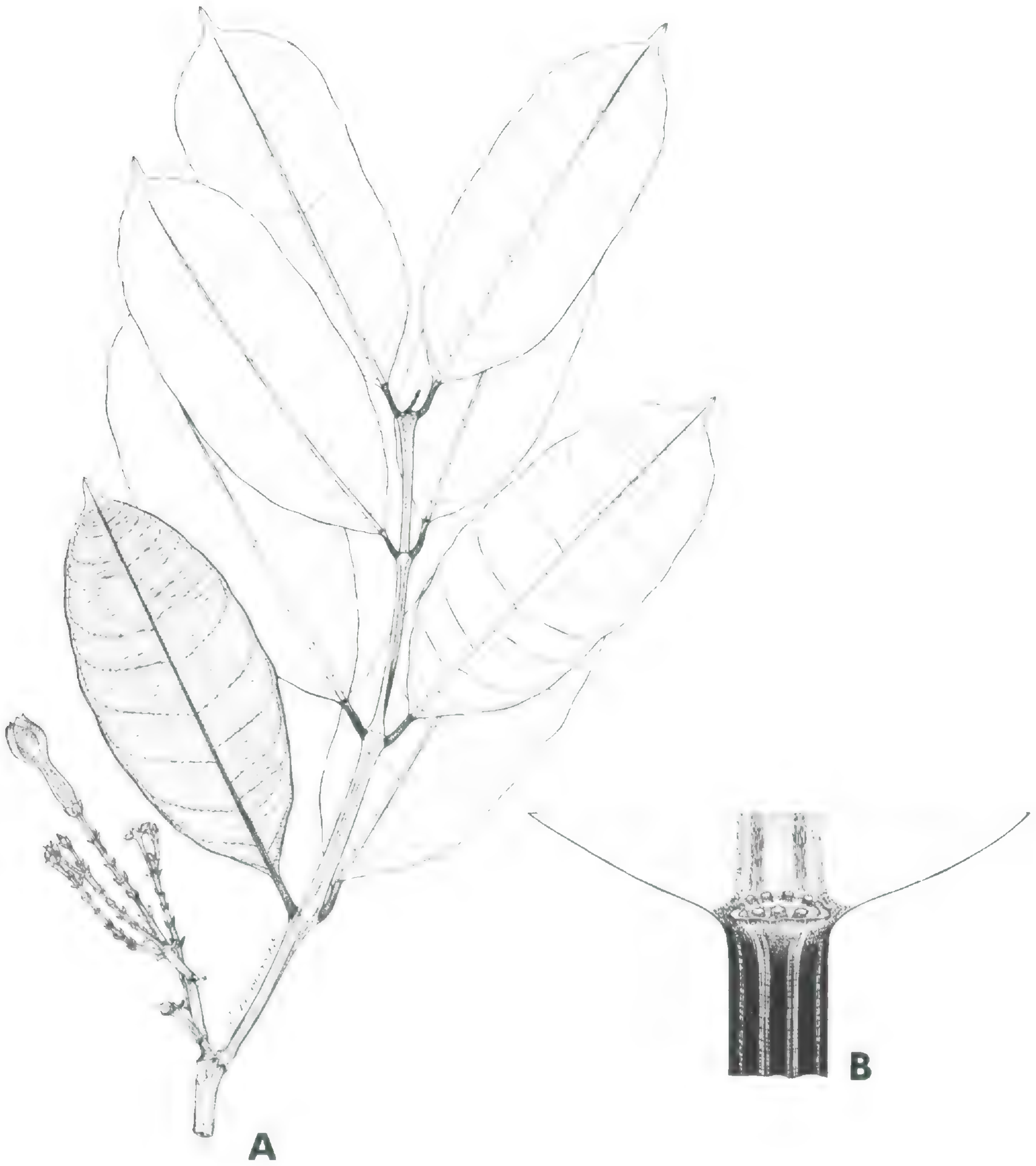

FIGURE 17. *Allomarkgrafia plumeriaefolia* Woodson.—A. Habit (× ½).—B. Upper surface of leaf showing glands at base of midrib (× 6). [After *Lewis et al. 3162* (MO).]

separate or ± concrescent, the style 1, the stigma fusiform-umbraculiform. *Fruit* apocarpous, of 2 follicles, terete; seeds numerous, dry, subscaphiform, comose apically.

A genus of about 10 species in tropical America.

Useful reference:

Woodson, R. E., Jr. *Mesechites*. Pp. 629–645 *in* "The American genera of the Echitoideae." Ann. Missouri Bot. Gard. 20: 605–790. 1933.

Mesechites trifida (Jacq.) Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 151. 1860.—FIG. 18.

Echites trifida Jacq., Enum. Syst. Pl. Carib. 13. 1760.

Lianas, glabrous or sometimes sparsely puberulent on the younger parts. *Leaves* elliptic, sometimes ovate to ovate-oblong, mucronate, weakly rounded,

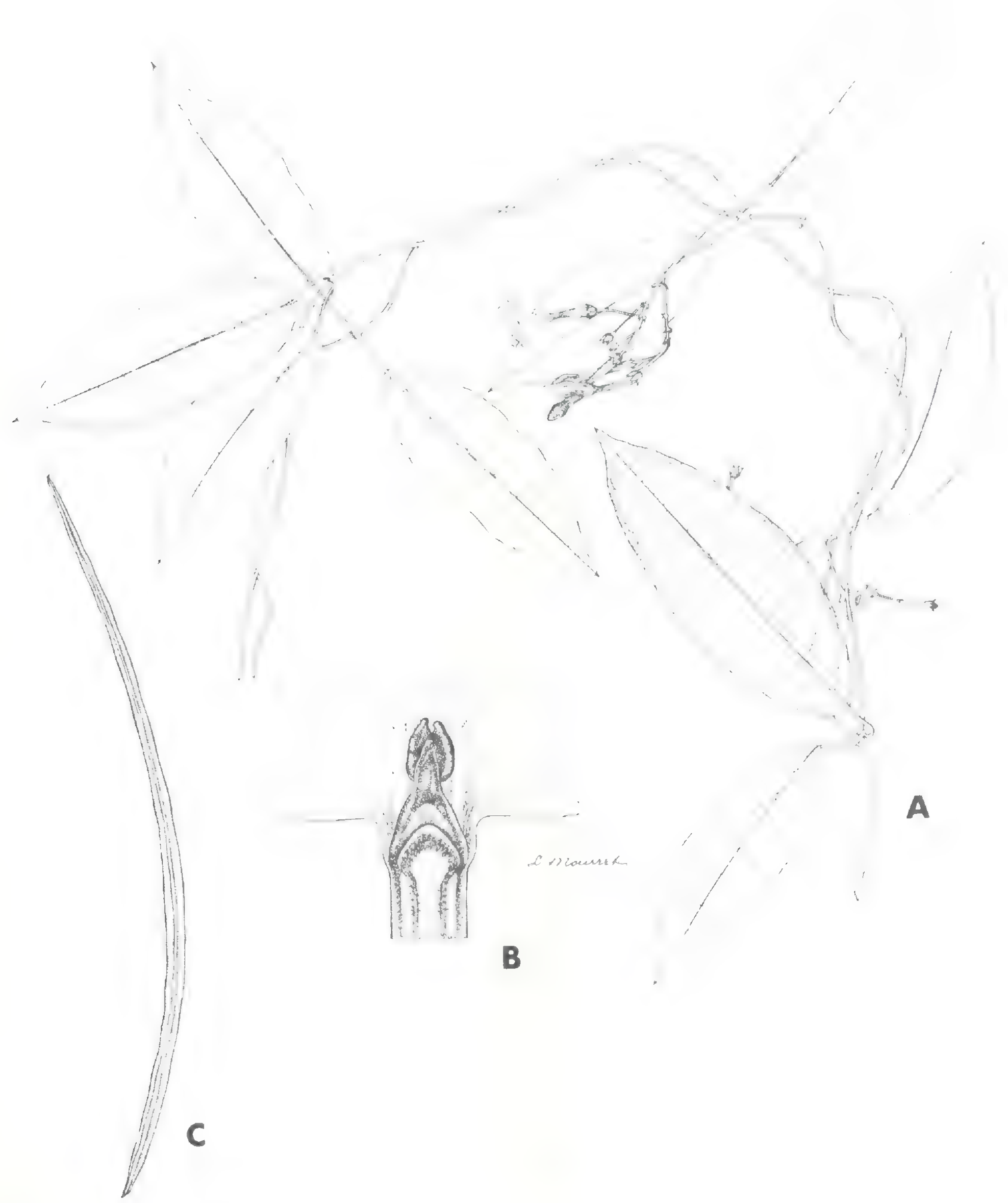

FIGURE 18. *Mesechites trifida* (Jacq.) Müll.-Arg.—A. Habit with inflorescence (× 1/2).—B. upper surface of leaf with glands at base of midrib (× 12). C. Fruit (× 3/8). [A, B, after *Woodson et al. 1549* (MO); C, after *Hunter & Allen 526* (MO).]

shallowly cordate, or ± obtuse basally, to 11 cm long and 5.5 cm wide, glabrous, firmly membranaceous; petioles 0.5–2.5 cm long. *Inflorescences* bostrychoid, 15–25-flowered, the peduncles ca. 1.5–4 cm long. *Flowers* with the pedicels 3–11 mm long; bracteoles minute; calyx-lobes ± equal, deltoid, delicately fimbriolate, 2–4 mm long, the squamellae 7–10, ± alternate; corolla green-white or green-yellow, the tube ca. 15–25 mm long, ± expanded at the level of stamen attachment, the lobes oblong or obovate, ca. 8–12 mm long and 5–6 mm wide, reflexed; anthers ca. 4 mm long, the connective densely pilose; nectaries 5 and separate, or fewer and concrescent, the stigma fusiform-umbraculiform. *Follicles* 15–40 cm long, glabrous, narrowly terete; seeds linear, ca. 1 cm long, comose, the hairs 2–3 cm long.

Southern Mexico, Central America, and northern and northeastern South America.

BOCAS DEL TORO: 10 15 mi. inland from mouth of Río Changuinola, *Lewis et al.* 889 (MO). CANAL ZONE: Barro Colorado Island, *Aviles 71, Bangham* 573 (both F), *Croat 4401, 6698, 6877, 8127* (all MO), *Shattuck 591, Wetmore & Abbe 31, 136, Woodworth & Vestal* 573 (all F). Near beach at Fort Kobbe, *Duke 4184, 4218* (both MO). In government forest along Las Cruces Trail, *Hunter & Allen 706, 767* (both MO). COCLE: El Valle de Anton and vicinity, *Siebert 492* (MO). Mountains beyond La Pintada, *Hunter & Allen* 526 (MO). PANAMA: SE slope of Cerro Campana, *Lewis et al. 3132* (MO). Chimán, *Lewis et al. 3318* (MO). About 10 mi. W of Hacienda La Joya, *Dodge et al. 16876* (MO). Vicinity of San Carlos, *Allen 1137* (MO). Taboga Island, *Macbride 2774, 2777* (both F), *Woodson et al. 1549* (MO). SAN BLAS: Mainland opposite Ailigandi from mouth of Río Ailigandi to 2.5 mi. inland, *Lewis et al. 182* (MO). VERAGUAS: Hills W of Soná, *Allen 1022* (MO). PROVINCE UNKNOWN: Forest near Casa Larga, *Allen s.n.* (MO).

18. MANDEVILLA

Mandevilla Lindl., Bot. Reg. n.s. 3: *pl.* 7. 1840.

Exothostemon G. Don, Gen. Syst. 4: 82. 1838, *pro parte*.

Lianas, undershrubs or herbs, lacticiferous. *Leaves* opposite or verticillate, glandular at the base of the midrib or along its entire length, rarely non-glandular, pinnately-nerved; petioles somewhat perfoliate, glandular in the axils. *Inflorescences* racemose, rarely obscurely compound, mostly axillary. *Flowers* medium-sized; bracteoles present; calyx 5-lobed, the lobes equal to subequal, bearing 1 to many alternate, opposite, or indefinitely distributed squamellae within; corolla infundibuliform, salverform, or tubular-salverform, without appendages, the tube straight or ± gibbous, the limb 5-lobed, dextrorsely convolute; stamens 5, ± included, or half-exserted, the anthers connivent and agglutinated to the stigma, with an enlarged connective characterized by a pedestal-like projection; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules numerous, the nectaries 2–5, rarely absent, separate or ± united basally, the style 1, the stigma pentagonal-umbraculiform. *Fruit* apocarpous, of 2 follicles, continuous to moniliform; seeds numerous, dry, truncate, comose apically.

A large genus of 100 or more species in Mexico, Jamaica, and Central and South America.

In Panama the four species of the genus are readily segregated from the remaining Apocynaceae by their cordate to subhastate leaf bases and the elongated tube of the corolla.

Useful reference:

Woodson, R. E., Jr. *Mandevilla*. Pp. 645–777 *in* "The American genera of the Echitoideae." Ann. Missouri Bot. Gard. 20: 605–790. 1933.

a. Corolla tube straight; leaves glandular at the base of the midrib. . . . 1. *M. veraguasensis*
aa. Corolla tube ± gibbous or arcuate; leaves sparsely glandular along the entire midrib.
b. Corolla infundibuliform . . . . . 2. *M. hirsuta*
bb. Corolla salverform.
c. Bracts scarious, 1–5 mm long. . . . . 3. *M. subsagittata*
cc. Bracts foliaceous or petaloid, 10–30 mm long. . . . . 4. *M. villosa*

1. **Mandevilla veraguasensis** (Seemann) Hemsley, Biol. Centr.-Amer., Bot. 2: 317. 1881.

Echites veraguasensis Seemann, Bot. Voy. Herald 168. 1854.

Lianas, the younger stems sparsely pubescent. *Leaves* opposite, ovate to ovate-elliptic, acuminate, cordate basally, to 11 cm long and 6 cm wide, sparsely pubescent on the veins of both surfaces, firmly membranaceous, glandular at the base of the midrib; petioles to 3 cm long, sparsely pubescent, weakly perfoliate, sparsely glandular in the axils. *Inflorescences* racemose, axillary and alternate, several (5–9) flowered, the peduncle ca. 2–3 cm long. *Flowers* with the pedicels 1–4 cm long; bracteole 1, deltoid, ca. 1–1.5 mm long; calyx-lobes ± equal, ovate, the margins sparsely fimbriolate, ca. 4–6 mm long, bearing groups of alternately placed squamellae; corolla subinfundibuliform, green with red lobes, the tube proper straight, 25–30 mm long, the throat narrowly conic, ca. 9–12 mm long, pubescent within, the lobes obliquely obovate, 25–30 mm long; stamens half-exserted, the filaments short and pubescent, the anthers and connective ca. 6–7 mm long, the connective truncate; nectaries 5, about half as high as the ovary. *Follicles* unknown.

Costa Rica, Panama, Colombia, Venezuela, and Ecuador.

CHIRIQUI: Forests around El Boquete, *Pittier 3147* (F, MO, US). Upper Río Chiriquí Viejo, *P. White 347* (MO). Volcán de Chiriquí Viejo, *Allen 981* (MO).

2. **Mandevilla hirsuta** (L. Rich.) K. Schum., Nat. Pfl. 4(2): 171. 1895.—FIG. 19.

Echites hirsuta L. Rich., Act. Soc. Hist. Nat. Paris 1: 107. 1792.

Lianas, moderately to densely pubescent, especially on the younger parts, the hairs uniseriate, white to brown. *Leaves* opposite, glandular along the midrib, elliptic to oblong-obovate, acuminate, auriculate basally, to 13 cm long and 7 cm wide, membranaceous, sparsely pubescent above and the hairs ± straight, more densely pubescent beneath and the hairs curved; petioles 1–3.5 cm long. *Inflorescences* racemose, axillary, 5–10(–17) cm long. *Flowers* with the pedicels 2–5 mm long; bracts elongate-rhomboid, pubescent, chartaceous, 8–15 mm long; calyx-lobes ± equal, ± lanceolate, pubescent, ca. 8–10 mm long, each with a single oppositely placed squamella; corolla infundibuliform, weakly arcuate, yellow with a red or maroon throat, pubescent externally, especially in bud, the tube proper 25–32 mm long, pubescent within, the throat conic, 18–20 mm

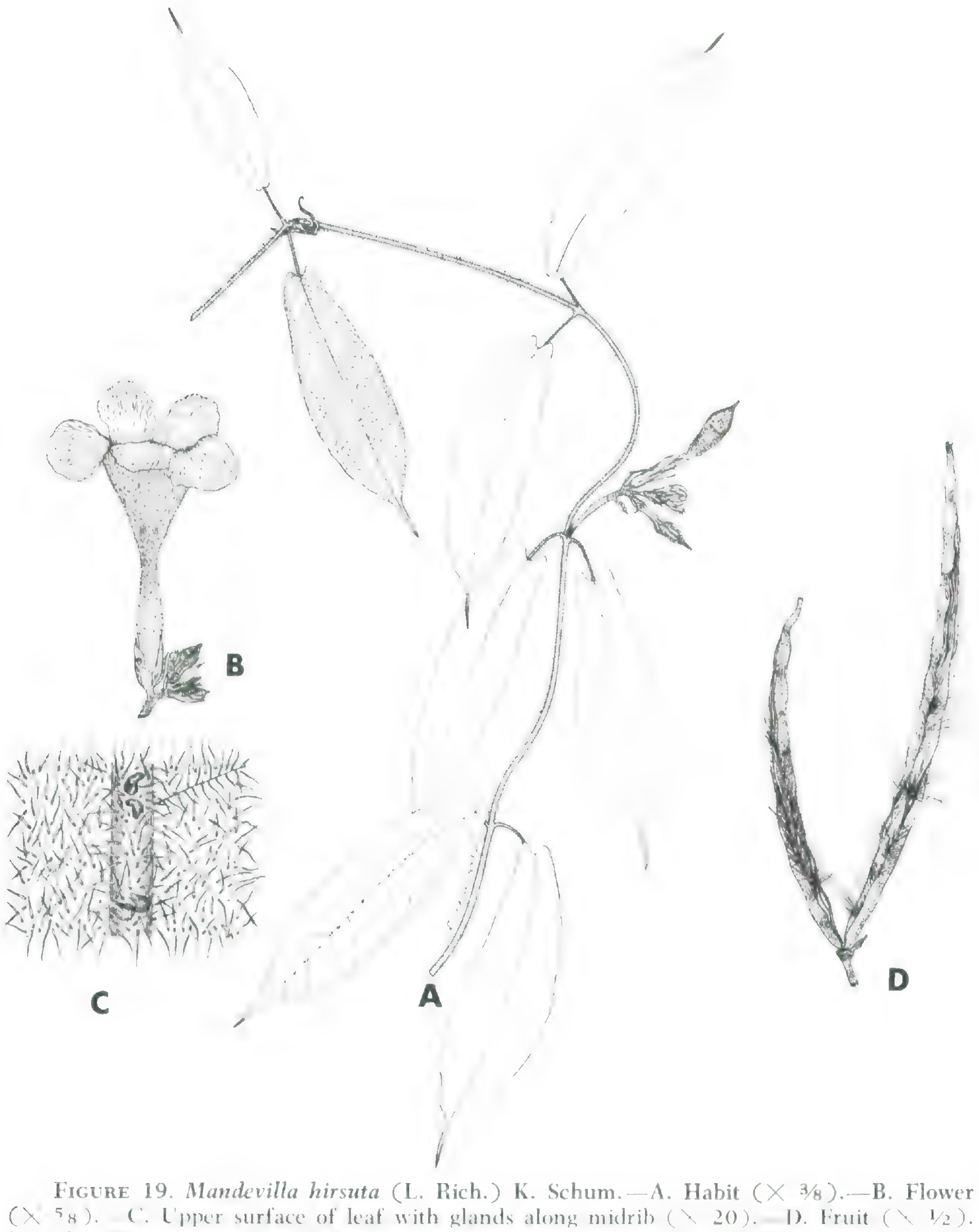

FIGURE 19. *Mandevilla hirsuta* (L. Rich.) K. Schum.—A. Habit (× 3/8).—B. Flower (× 5/8).—C. Upper surface of leaf with glands along midrib (× 20).—D. Fruit (× 1/2). [A, after *Tyson 1624* (MO); B C, after *Woodson et al. 1246* (MO); D, after *Allen 1020* (MO).]

long, the lobes ± obliquely dolabriform, 12–16 mm long and 9–12 mm wide, slightly spreading; stamens included, attached at the base of the corolla throat, the anthers ca. 2.5 mm long, the connective obtusely 2-lobed; nectaries concrescent, almost as high as the ovary, the stigma conspicuously umbraculiform. *Follicles* moniliform, terete, pubescent, to 15 cm long; seeds somewhat canaliculate, 10–11 mm long.

A common and widespread species in Central and South America.

CANAL ZONE: 5 mi. NW of Cocolí, *Tyson 1624* (MO). Vicinity of former town of Empire, Culebra Cut and vicinity, *Hunter & Allen 779* (F, MO). Fort Davis, *Higgins 340* (MO). Howard AFB, SE of Kobbe Beach, *Oliver & MacBryde 1877* (MO). CHIRIQUI: Vicinity of El Boquete, *Allen 1020* (MO), *Davidson 637* (F, MO). Vicinity of Río Tinta, along main highway, *Woodson et al. 381* (MO). COCLE: Between Las Margaritas and El Valle, *Woodson et al. 1246* (MO). HERRERA: 10 mi. S of Ocú, *Tyson et al. 2871* (MO). LOS SANTOS: Loma Prieta, Cerro Grande, *Lewis et al. 2211* (MO). PANAMA: Thickets and forests near Arraíjan, *Woodson et al. 778* (MO). Cerro Azul, *Tyson 2130* (MO). Cerro Campana, bald savanna-like areas along road to top, *Duke 5974* (MO); elfin forest beyond Motel Su-Lin, *Duke 8654* (MO); wooded area along road, *Ebinger 363* (MO). Cerro Jefe, cloud forest, *Elias & Hayden 1794* (MO); *Clusia* forest, *Tyson et al. 3234* (MO); 2–3 mi. S of Goofy Lake, *Lewis et al. 281* (MO); 10–13 mi. beyond Goofy Lake, *Duke 8014, 9421, 9428*, (all MO). SAN BLAS: Inland from airport at Mandinga, *Duke 8920* (MO).

Woodson (Ann. Missouri Bot. Gard. 20: 767. 1933) considered this species unusually uniform for one of such a wide geographical distribution. He regarded the complex synonomy as due to the insufficient material and poor bibliographical aids of earlier authors.

3. **Mandevilla subsagittata** (Ruiz & Pavon) Woodson, Ann. Missouri Bot. Gard. 19: 69. 1932.

Echites subsagittata Ruiz & Pavon, Fl. Peru. 2: 19. 1799.

Lianas, mostly glabrous or sometimes moderately pubescent. *Leaves* opposite, sparsely glandular along the midrib, elliptic or oblong-elliptic, acute, subhastate to auriculate basally, to 8 cm long and 3.5 cm wide, glabrous or sparsely pubescent on the veins, membranaceous; petioles ± pubescent, 2–5 mm long. *Inflorescences* racemose, axillary, to ca. 9 cm long. *Flowers* with the pedicels 3–5 mm long; "bracts scarious, lanceolate, 1–5 mm. long"[7]; calyx lobes subequal, deltoid, ca. 1 mm long, each bearing 1 oppositely placed squamella; corolla salverform, yellow with a red throat, the tube ca. 25–30 mm long, gibbous, somewhat pubescent near the top, the lobes obovate to oblong, ca. 12–16 mm long and 9–12 mm wide, spreading, sparsely pubescent beneath; stamens included, attached near the top of the corolla throat, the anthers ca. 1.5 mm long; nectaries 5, sometimes fewer and concrescent, ca. half as high as the ovary. *Follicles* unknown.

Mexico, Central America, and northern South America.

CANAL ZONE: Barro Colorado Island, *Brown 191* (F). Frijoles, *Ebinger 637* (MO). West end of island (?), *P. White 132* (MO). CHIRIQUI: Boquete, *Davidson 847* (F, MO). PANAMA: Near Chepo, *Pittier 4756* (F).

4. **Mandevilla villosa** (Miers) Woodson, Ann. Missouri Bot. Gard. 19: 70. 1932.

Laseguea villosa Miers, Apoc. S. Amer. 250. 1878.

Lianas, the younger parts pubescent, the hairs uniseriate, brown or white. *Leaves* opposite, sparsely glandular along the midrib, elliptic to obovate, acute to finely acuminate, shallowly cordate to auriculate basally, to 8 cm long and 4 cm

[7]Quoted from R. E. Woodson, Jr., N. Amer. Fl. 29: 155. 1938.

wide, glabrous to sparsely pubescent above, glabrous to densely softly pubescent beneath, membranaceous; petioles ca. 1–2 cm long, pubescent. *Inflorescences* racemose, irregular, axillary, the peduncles ca. 1–2 cm long. *Flowers* with the pedicels 2–4 mm long; bracts elongate-ovate or lanceolate, acuminate, pubescent on the margins and the inner surface, 1–3 cm long; calyx-lobes separate almost to the base, ± equal, deltoid, acuminate, ca. 1.5–2 mm long, each bearing 1 oppositely placed lacerate squamella; corolla salverform, weakly arcuate, yellow with a red or peach throat, the tube ca. 25–35 mm long, pubescent at the level of stamen attachment, the lobes obliquely oblong, ca. 18–22 mm long and 8–11 mm wide, spreading; stamens ± included, borne near the orifice of the throat, the anthers ca. 2.5 mm long, the connective obtusely 2-lobed; nectaries ± concrescent. *Follicles* somewhat moniliform, terete, sparsely pubescent, ca. 10–15 cm long; seeds awl-shaped, ca. 8 mm long.

Southern Mexico, Central America, and Venezuela.

BOCAS DEL TORO: Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 1993* (MO). CANAL ZONE: Cerro Gordo, near Culebra, *Pittier 3736* (F, MO, US). France Field, *Stevens 1006* (MO). Fort Sherman, vicinity of Hill C-6, *Duke 4362* (MO). Vicinity of Miraflores Lake, *G. White 156* (MO). Sabanas along drowned Río Azote Caballo, *Dodge et al. s.n.* (MO). COCLE: Between Las Margaritas & El Valle, *Woodson et al. 1749* (MO). PANAMA: Thickets near Capira, *Woodson et al. 1227* (MO). Pedro Gonzalez Island, *Allen 2589* (MO). San José Island, *Johnston 52* (MO).

19. FORSTERONIA

Forsteronia G. Meyer, Prim. Fl. Essequeb. 133. 1818.

Lianas, rarely becoming subshrubs, lacticiferous. *Leaves* opposite, rarely ternate or quadrate, frequently with an inconspicuous pit in the axils of the midrib and principal veins beneath, glandular at the base of the midrib or rarely non-glandular, pinnately-nerved; mostly petiolate and inconspicuously stipulate. *Inflorescences* thyrsiform, dichasial, or ± spicate, axillary and opposite, or terminal. *Flowers* small; bracteoles mostly present; calyx 5-lobed, the lobes essentially equal, bearing 1 to several squamellae within, or rarely the squamellae apparently absent; corolla rotate, subrotate, or ± campanulate, without appendages, the limb 5-lobed, dextrorsely or rarely sinistrorsely convolute; stamens 5, included to wholly exserted, the filaments with or without appendages, free or agglutinated to the style, the anthers connivent and agglutinated to the stigma, the connective enlarged, characterized by a pedestal-like projection at the base; gynoecium 2-carpellate, apocarpous or rarely syncarpous, the ovary superior, the ovules numerous, the nectaries 5, distinct or concrescent, the style 1, the stigma fusiform to subcapitate. *Fruit* apocarpous or rarely somewhat agglutinated, of (1–)2 follicles, ± slender; seeds numerous, dry, truncate, comose apically.

A large genus of about 50 species centering in northeastern South America, but found also in Mexico, Central America, parts of the West Indies, and southward to Argentina.

Two species, *Forsteronia spicata* (Jacq.) G. Meyer and *F. viridescens* Blake, are found in Panama. Woodson (Ann. Missouri Bot. Gard. 22: 153–224. 1935) reported three species: *F. spicata, F. myriantha* Donn. Sm., and *F. chiriquensis*

Woodson. However, I have not seen specimens which correspond to the latter two species; the drawings and specimens which Woodson cited are not to be found at the Missouri Botanical Garden.

a. Inflorescences spicate, sometimes weakly thyrsiform basally; leaves membranaceous, a tuft of hair in the axils of the veins beneath . . . . . 1. *F. spicata*
aa. Inflorescences conspicuously thyrsiform; leaves subcoriaceous, glabrous . . . 2. *F. viridescens*

1. **Forsteronia spicata** (Jacq.) G. Meyer, Prim. Fl. Essequeb. 135. 1818.—Fig. 20.

Echites spicata Jacq., Enum. Syst. Pl. Carib. 13. 1760.

Lianas, sometimes shrub-like, the younger stems softly pubescent. *Leaves* opposite, glandular at the base of the midrib, elliptic to obovate, to 16 cm long and 7 cm wide, ± glabrous to sparsely pubescent above, pubescent on the veins

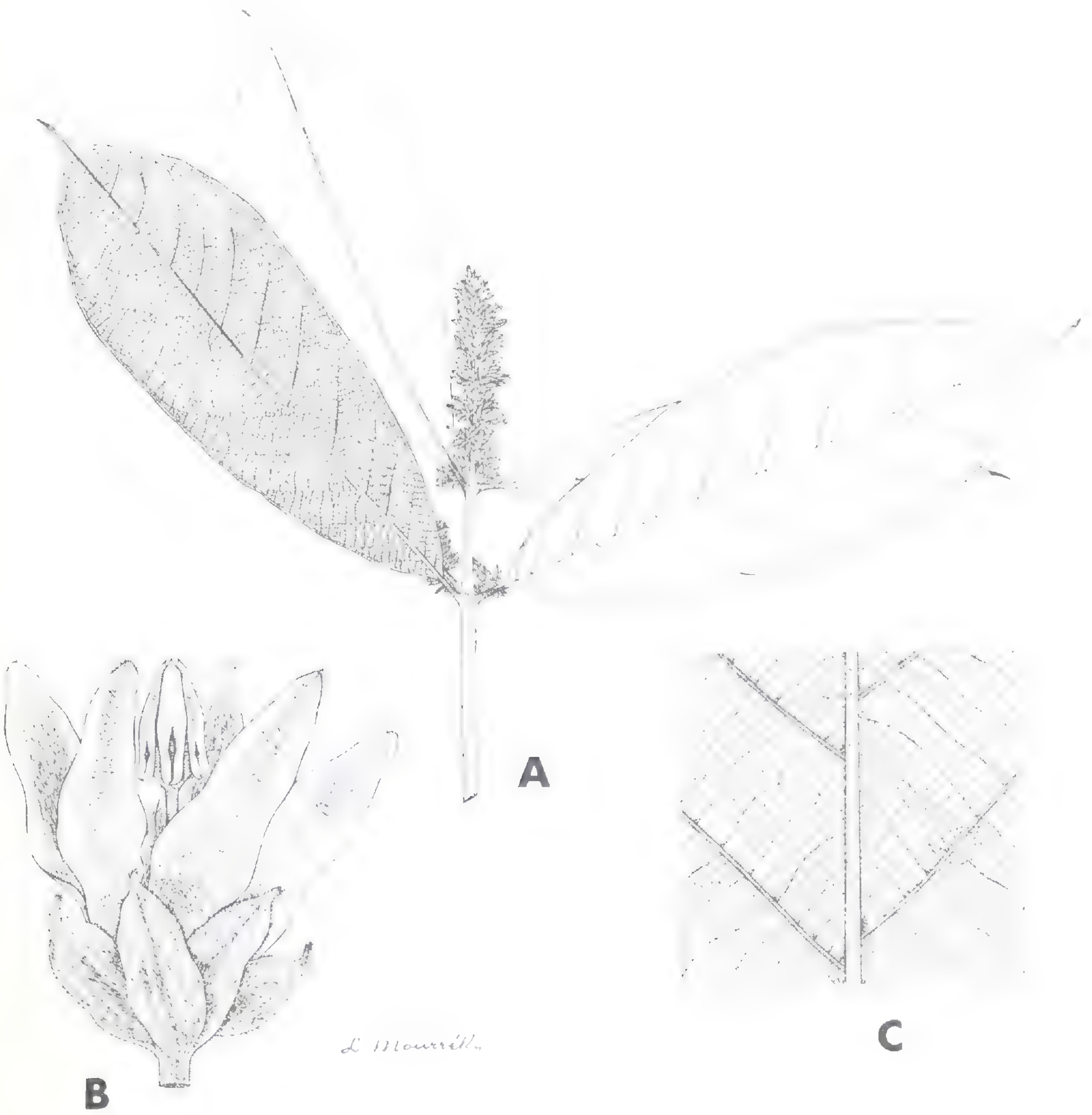

Figure 20. *Forsteronia spicata* (Jacq.) Meyer.—A. General habit with inflorescence (× ½).—B. Flower (× 7).—C. Undersurface of leaf showing tufts of hair in axils of veins (× 2 1/10). [After *Erlanson* 258 (US).]

beneath, a tuft of hair in the axils, membranaceous; petioles ca. 5–9 mm long. *Inflorescences* spicate, thyrsiform near the base, terminal or axillary and opposite, to ca. 6 cm long. *Flowers* ± sessile; calyx lobes deltoid, somewhat keeled, ca. 2.5–3.5 mm long, the margins fimbriolate, bearing 1–2 squamallae within; corolla subcampanulate, white, glabrous externally, the tube ca. 2 mm long, densely pubescent within, the lobes oblong, ca. 4 mm long; stamens wholly exserted, the filaments ca. 2 mm long, the anthers ca. 2 mm long; ovary apocarpous basally, syncarpous above, pubescent, the nectaries ca. 5, shorter than the ovary, the stigma pentagonal. *Follicles* ± united, continuous, scabrous, ca. 17 cm long; seeds ca. 1 cm long, the testa pubescent.

Southern Mexico, Central America, Cuba, and Colombia.

COCLE: 1–5 mi. S of Antón on road to coast, *Tyson & Blum 2574* (MO). PANAMA: San José Island, *Erlanson* 95, 258 (both US). Taboga Island, *Woodson et al. 1551* (MO).

2. **Forsteronia viridescens** Blake, Contr. Gray Herb. 52: 80. 1917.

Lianas, the younger stems and inflorescences ferrugineous-pubescent, lactiferous. *Leaves* opposite, glandular at the base of the midrib above, ± elliptic, acute or shortly acuminate, obtuse basally, to 12.5 cm long and 6 cm wide, ± glabrous on both surfaces, subcoriaceous; petioles 2–5 mm long. *Inflorescences* thyrsiform, axillary and opposite or terminal, to 8 cm long. *Flowers* subsessile or with pedicels to 1.5 mm long; bracteole single, deltoid and keeled, 1–1.5 mm long, pubescent; calyx-lobes deltoid, somewhat keeled, ca. 1 mm long, pubescent, bearing 2 squamellae within; corolla subcampanulate, cream, softly pubescent externally, the tube ca. 1 mm long, with a ring of hairs near the orifice, the lobes oblong, ca. 2 mm long; stamens half-exserted, the filaments free, ca. 0.5 mm long, the anthers ca. 1 mm long, slightly barbellate near the apex; ovary apocarpous, slightly papillate, nectaries concrescent, almost as high as the ovary, the stigma fusiform and acute. *Follicles* separate (?) slender, weakly moniliform, ferrugineous-tomentulose, ca. 11–23 cm long; seeds 12–15 mm long.

Apparently only from Guatemala, British Honduras, and Panama.

PANAMA: San José Island, *Erlanson* 339 (US), *Johnston 581, 650* (both MO, US).

In my opinion, there is some doubt about the distinction between *Forsteronia viridescens* and *F. myriantha* Donn. Sm.

20. MALOUETIA

Malouetia A. DC., Prodr. 8: 378. 1844.

Shrubs, or small trees, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved, pitted beneath in the axils of the midrib and principal nerves; petiolate and usually estipulate. *Inflorescences* umbellate, terminal or sometimes axillary, few- to several-flowered. *Flowers* small to medium-sized; calyx 5-lobed, the lobes ± equal, bearing 1–2 alternately placed squamellae within; corolla salverform, without appendages, the orifice sometimes conspicuously callose-thickened, the limb 5-lobed, dextrorsely convolute; stamens 5, exserted or included, the anthers connivent and agglutinated to the stigma, with an enlarged connective character-

ized by a tuft of hair; gynoecium 2-carpellate, apocarpous, the ovary superior, ovules many, nectaries 5, separate or ± connate basally, style 1, the stigma fusiform-subcapitate. *Fruit* apocarpous, of 2 follicles, or rarely 1 by abortion, ± spreading, slender to broadly fusiform; seeds many, dry, glabrous or pubescent, but not comose apically.

A genus of about 20 species, mostly in northeastern South America; one species is found in Central America, one on Cuba and St. Vincent, and two in Africa.

Useful reference:

Woodson, R. E., Jr. *Malouetia.* Pp. 238–270 *in* "The American genera of Echitoideae." Ann. Missouri Bot. Gard. 22: 153–306. 1935.

Malouetia guatemalensis (Müll.-Arg.) Standley, Jour. Washington Acad. Sci. 15: 459. 1925.—Fig. 21.

Stemmadenia guatemalensis Müll.-Arg., Linnaea 30: 410. 1860.
Malouetia panamensis Van Heurck & Müll.-Arg. *in* Van Heurck, Obs. Bot. 185. 1871.

Trees, or sometimes shrubs, to 15 m, mostly glabrous. *Leaves* elliptic or sometimes ovate-elliptic, acuminate, obtuse basally, to 21 cm long and 9 cm wide, glabrous, firmly membranaceous to slightly coriaceous; petioles 3–8 mm long. *Inflorescences* umbellate, axillary or terminal, the peduncle ca. 2–5 mm long. *Flowers* with the pedicels ca. 3–5 mm long, minutely papillate; calyx-lobes ± equal, slightly keeled, minutely papillose, 1.5–2 mm long, bearing 1–2 squamellae; corolla white to greenish-white, minutely papillose, especially on the limb, the tube ca. 4–5 mm long, thickened and somewhat closed at the orifice, slightly expanded at the level of stamen attachment, the lobes obliquely oblong, ca. 7–9 mm long and 1.2–1.8 mm wide, spreading; stamens included, the anthers ca. 1.8 mm long; ovary softly pubescent, nectaries ± 5, the stigma fusiform. *Follicles* 2, widely diverging, broadly fusiform, ca. 10(–15) cm long; seeds compressed, ca. 2 cm long.

Central America.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 113* (F). Chiriquí Lagoon, *von Wedel 1189* (MO); Old Bank Island, *von Wedel 1870, 1892* (both MO); Water Valley, *von Wedel 862, 900, 1583, 1741* (all MO). CANAL ZONE: Barro Colorado Island, *Croat 7842, 7985, 8365, 8435* (all MO). Chagres, *Fendler 184* (MO). Galena Point, *Dwyer & Robyns 157* (MO). Forest along Río Indio de Gatún, *Pittier 2813* (F). DARIEN: Near Río Chucunaque, ca. 4 mi. below Yaviza, *Duke 4869* (MO). SAN BLAS: Mainland point opposite Mosquito Island, *Duke 8978* (MO).

21. NERIUM

Nerium L., Sp. Pl. 209. 1753.

Shrubs or small trees, lacticiferous. *Leaves* ternate, quaternate, or sometimes opposite, non-glandular, coriaceous; petiolate or subsessile, mostly glandular in the axils. *Inflorescences* thyrisform, terminal, many-flowered. *Flowers* showy, medium-sized; calyx 5-lobed, the lobes ± equal, mostly imbricate, bearing many squamellae within; corolla infundibuliform, the throat with 5-cleft petaloid appendages, the limb 5-lobed, the lobes dextrorsely convolute; stamens 5, slightly

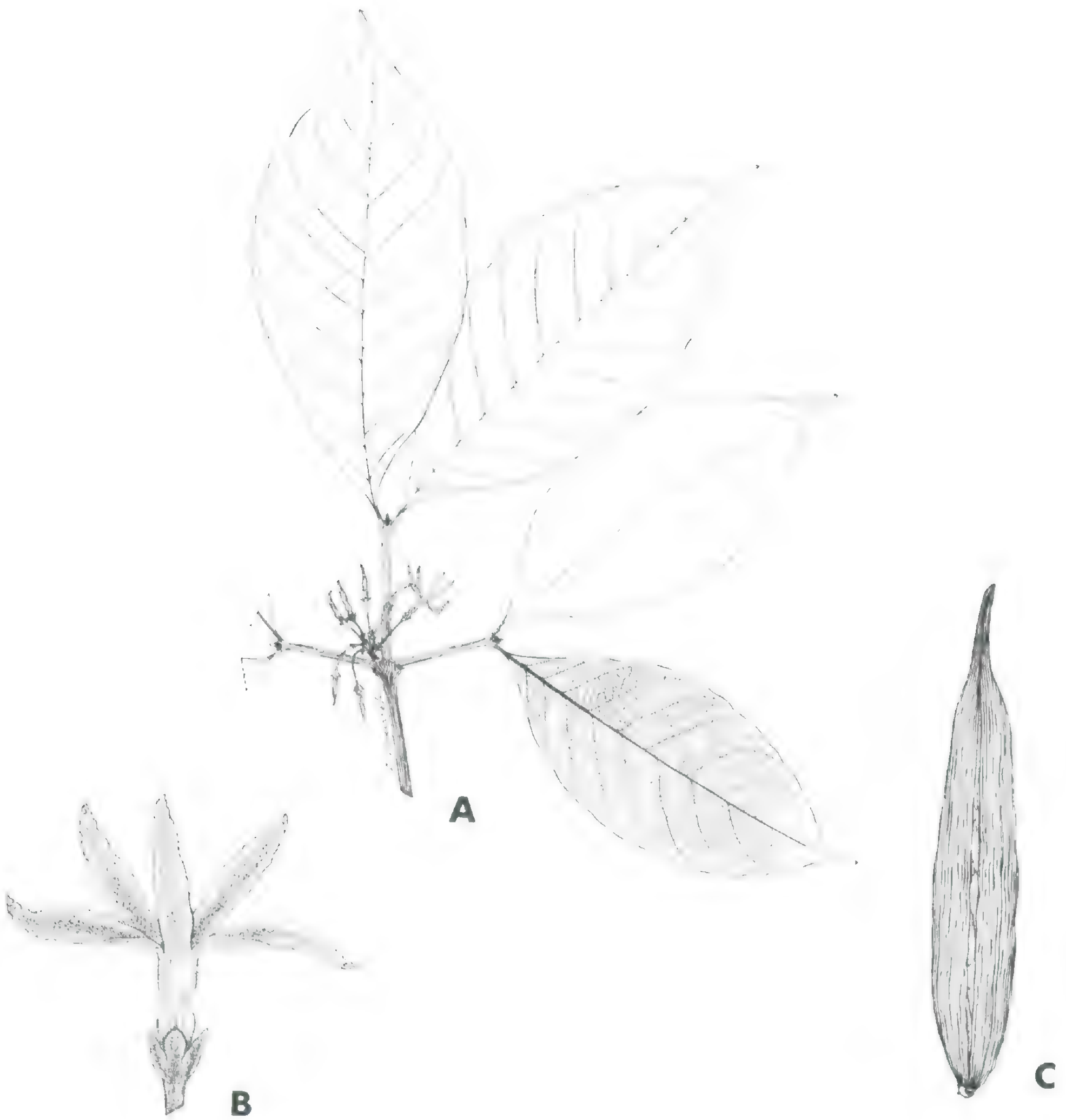

FIGURE 21. *Malouetia guatemalensis* (Müll Arg.) Standley. A. General habit with inflorescence (× ½).—B. Flower (× 2 2/5).—C. Fruit (× 3/5). [A–B, after *von Wedel 1892* (MO); C, after *Duke 4869* (MO).]

exserted, the anthers connivent and agglutinated to the stigma; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, without a nectary, the style 1, the stigma fusiform. *Fruit* apocarpous, of 2 follicles, ± stout; seeds many, dry, compressed, densely puberulent, comose apically.

A genus of about three species, native to the Mediterranean region and Asia.

Nerium oleander L., Sp. Pl. 209. 1753.—Fig. 22.

Shrubs, or small trees, the younger stems puberulent. *Leaves* mostly ternate, oblong-lanceolate, acute-acuminate, attenuate basally, to 20 cm long and 2.5 cm wide, puberulent beneath when young, the midrib pronounced, the lateral veins obscure; petioles 3–10 mm long, glandular in the axils. *Inflorescences* thyrsiform, the primary peduncle ca. 6–9 cm long. *Flowers* double or triple in Panama; pedi-

Figure 22. *Nerium oleander* L., flowering branch (× 7/8). [After *Standley* 30826 (US).]

cels 5–13 mm long, puberulent; bracteole 1, ovate, 4–5 mm long, variously placed; calyx-lobes ± ovate, somewhat keeled, ca. 5–7 mm long, pubescent, somewhat foliaceous and pinkish; corolla white or pink-orange to scarlet, "glabrous externally, the tube proper 8–12 mm long, about 1.5 mm in diameter at the base, the throat conic-campanulate, 9–10 mm long, about 7 mm in diameter at the orifice, the lobes obliquely obovate to obovate-oblong, 20–25 mm long, spreading; follicles relatively stout, 8–15 cm long."[8]

Native to the Mediterranean region, but widely cultivated and occasionally escaped in tropical America.

CANAL ZONE: Balboa, *Standley* 30826 (US). PANAMA: NE of Panama City, sabanas, *Bro. Paul* 217 (US).

22. PELTASTES

Peltastes Woodson, Ann. Missouri Bot. Gard. 19: 375. 1932.

Lianas, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved, peltate; petioles weakly perfoliate, glandular in the axils. *Inflorescences* aggregate-dichasial, axillary and opposite, or rarely terminal or subterminal, few- to several-flowered. *Flowers* mostly large and showy; bracteolate; calyx 5-lobed, the lobes equal or unequal, bearing many squamellae within; corolla infundibuliform, without appendages, the limb 5-lobed, dextrorsely convolute; stamens 5, the anthers connivent and agglutinated to the stigma, with an enlarged connective, characterized by a curved ridge; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries 5, separate, the style 1, the stigma capitate-fusiform. *Fruit* apocarpous, of 2 terete follicles; seeds many, dry, rostrate, comose apically.

A genus of about six species found in northern South America; one species in Panama and Costa Rica.

Peltastes isthmicus Woodson, Ann. Missouri Bot. Gard. 23: 187. 1936.—FIG. 23.

Lianas, stout, the stems brown-pubescent. *Leaves* broadly ovate, acute, peltate basally, to 26 cm long and 22 cm wide, sparsely pubescent on both surfaces, more so beneath when young, firmly membranaceous; petioles to 15 cm long, brown-pubescent to ± glabrous. *Inflorescences* aggregate-dichasial, axillary and opposite. *Flowers* with the pedicels 5–13 mm long, brown-pubescent; bracteoles oblong-spathiform, foliaceous, 12–20 mm long, variously placed on the pedicel; calyx-lobes subequal, oblong-ovate to oblong-obovate, 20–30 mm long and 8–12 mm wide; pale greenish-white, glabrous externally, the tube proper ca. 25–30 mm long, pubescent within, the throat conic, ca. 15–20 mm long, the lobes obliquely obovate, ca. 25–30 mm long; stamens included, attached low in the corolla throat, the anthers and connective ca. 11–12 mm long, appressed-pubes-

[8]Because both the Panamanian collections have double or triple sterile flowers, a direct quote was taken from Woodson, N. Amer. Fl. 29: 164 165. 1938.

FIGURE 23. *Peltastes isthmicus* Woodson, fruiting branch (× ½). [After *Pittier* 5125 (US).]

cent dorsally; nectaries somewhat distinct, almost as high as the ovary. *Follicles* stout, ca. 22 cm long, striate, irregularly ferrugineous-papillate; seeds ca. 15 mm long.

Costa Rica and Panama.

CANAL ZONE: Between Madden Dam and Casa Larga, *Allen s.n.* (MO, US). CHIRIQUI: Trail from San Felix to Cerro Flor, *Allen 1945* (MO, US). Vicinity of San Felix, *Pittier 5125* (US, holotype), Dec. 1911 (F).

Johnston (Sargentia 8: 246. 1949) reports flowers to 8 cm long on collections from San José Island.

23. ODONTADENIA

Odontadenia Benth., Jour. Bot. (Hooker) 3: 242. 1841.

Lianas, rarely becoming suberect, lacticiferous. *Leaves* opposite, sometimes alternate above, non-glandular, pinnately-nerved; petiolate, stipulate or estipulate. *Inflorescences* thyrisform to ± scorpioid, few- to many-flowered, axillary and opposite, or terminal. *Flowers* mostly showy; calyx 5-lobed, the lobes ± equal to conspicuously unequal, bearing few to many alternate or indefinitely distributed squamellae within; corolla infundibuliform to salverform, without appendages, the limb 5-lobed, the lobes dextrorsely convolute; stamens 5, ± included, the anthers connivant and agglutinated to the stigma, with an enlarged connective, characterized by a vertical crest; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries 5, connate basally, rarely ± separate, the style 1, the stigma fusiform, subcapitate, or 5-digitate. *Fruit* apocarpous, of 2 follicles, terete or compressed; seeds many, dry, truncate, comose apically.

A genus of about 26 species centering in Brazil and Peru, but found in most of tropical America.

Useful reference:

Woodson, R. E., Jr. *Odontadenia.* Pp. 270–306 *in* "The American genera of Echitoideae." Ann. Missouri Bot. Gard. 22: 153–306. 1935.

a. Stipules broadly ovate, ca. 2–3 mm long; calyx lobes unequal . . . . . 1. *O. puncticulosa*
aa. Stipules apparently absent, or greatly reduced; calyx lobes + equal . . . . 2. *O. grandiflora*

1. **Odontadenia puncticulosa** (L. Rich.) Pulle, Enum. Pl. Surinam 383. 1906.—FIG. 24A.

Echites puncticulosa L. Rich., Act. Soc. Hist. Nat. Paris 1: 107. 1792.

Lianas, the mature stems lenticellate and glabrous, the younger stems softly puberulent. *Leaves* ovate to sometimes elliptic, shortly acuminate, slightly rounded basally, to 21 cm long and 11 cm wide, ± glabrous, subcoriaceous; petioles stout, to 1.5 cm long, stipules 2, broadly ovate, softly puberulent, ca. 2–3 mm long. *Inflorescences* thyrsiform, axillary and opposite, or terminal. *Flowers* with the pedicels to 3 cm long; bracteoles ovate, puberulent, ca. 3–4 mm long; calyx-lobes unequal, ovate to ovate-oblong, 4–8 mm long, pubescent, the margins fimbriolate, each bearing several alternately placed squamellae within; corolla infundibuliform, green and white, minutely papillate externally, especially so in

FIGURE 24. *Odontadenia*.—A. *O. puncticulosa* (A. Rich.) Pulle, flower (× 4/5). [After *Porter et al. 4733* (MO).] —B. *O. granditlora* (G. Meyer) Miq., general habit with flower (× 4/5). [After *Croat 8549* (MO).]

bud, the tube proper ca. 15 mm long, pubescent near the apex, the throat only weakly expanded, ca. 30–35 mm long, the lobes broadly ovate, ca. 20 mm long; stamens wholly included, attached at the base of the corolla throat, the filaments short, pubescent, the anthers ca. 5–6 mm long, pubescent dorsally; ovary puberulent, the nectaries concrescent, entire, covering the ovary, the styles appearing almost separate, the stigma ± fusiform. *Folicles* terete, stout, puberulent, ca. 9 cm long; seeds ca. 12–14 mm long.

Costa Rica, Panama, Surinam, and Brazil.

CANAL ZONE: Barro Colorado Islands, *Croat* 8633 (MO), *Kenoyer* 502 (US). COLON: Santa Rita Ridge between Transisthmian Highway and end of road, *Porter et al.* 4733 (MO).

2. **Odontadenia grandiflora** (G. Meyer) Miq., Stirp. Surinam. Select. 166. 1851.—Fig. 24B.

Echites grandiflora G. Meyer, Prim. Fl. Essequeb. 131. 1818.

Lianas, ± glabrous. *Leaves* elliptic to weakly obovate, acuminate, acute or occasionally retuse (diseased?), obtuse basally, to 21 cm long and 9 cm wide, glabrous, firmly membranaceous to chartaceous; petioles ca. 1–2 cm long, weakly perfoliate, stipules obsolete. *Inflorescences* cymose, irregularly branched, axillary or terminal, the peduncles 4–9 cm long. *Flowers* with the pedicels 10–20 mm long; bracts deltoid, minute; calyx-lobes ± equal, ovate to broadly ovate, 3.5–5 mm long, each with 1–2 squamellae; corolla infundibuliform, yellow, gold or white, often flushed with red or orange, the tube proper ca. 5–7 mm long, constricted above the level of stamen attachment, the throat conic, 25–32 mm long, the lobes obliquely obovate, 20–30 mm long and 20–25 mm wide, spreading; stamens wholly included, the filaments pubescent at the bases, the anthers ca. 5–6 mm long, pubescent dorsally; nectaries somewhat woody, lacerate, the stigma fusiform. *Follicles* unknown for Panama.

Costa Rica, Panama, and tropical South America.

CANAL ZONE: Barro Colorado Island, *Bangham* 519, 561 (both F), *Croat* 5145, 8315, 8450, 8549 (all MO), *Shattuck* 693, *Wetmore & Abbe* 221, *Woodworth & Vestal* 662 (all F). Near Frijoles, *Allen* 924 (MO, US). Government Forest along Las Cruces Trail, *Hunter & Allen* 448 (F, MO, US). Leion Hill Station, *Hayes* 663 (MO). N of island, Miraflores Lake, *P. White* 107 (MO). Near mouth of Río Chagres, *Allen* 888 (MO). Along Río Trinidad, *Pittier* 3976 (F, US). HERRERA: Vicinity of Chitré, *Allen* 1112 (US). PANAMA: Vicinity of Campana, *Allen* 3572 (MO, US). Wet savanna, E of Pacora, *Woodson et al.* 734, 739 (both MO). SAN BLAS: Vicinity of Permé, *Cooper* 261 (F, MO, US).

One immature collection of *Odontadenia* remains unnamed—SAN BLAS: Hills back of Puerto Obaldía, *Pittier* 4329 (US). Woodson (Ann. Missouri Bot. Gard. 22: 274. 1935) refers this collection to *O. cognata* (Stadelm.) Woodson, but it lacks, at least at this bud stage, the very unequal calyx lobes associated with that species.

24. FERNALDIA

Fernaldia Woodson, Ann. Missouri Bot. Gard. 19: 48. 1932.

Lianas, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved; petiolate, glandular in the axils. *Inflorescences* scorpioid, axillary and alternate, several- to many-flowered. *Flowers* medium-sized; calyx 5-lobed, the lobes equal to

subequal, bearing 1 oppositely placed squamella within; corolla infundibuliform, white, without appendages, the tube slightly gibbous to straight, the limb 5-lobed, dextrorsely convolute; stamens 5, included, the anthers connivent and agglutinated to the stigma, with an enlarged connective, characterized by a vertical crest; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries connate basally, unequally 4-lobed, the style 1, the stigma fusiform-capitate. *Fruit* apocarpous, of 2 follicles, terete; seeds many, dry, truncate, comose apically.

A genus of about four species in Mexico and Central America.

Fernaldia speciosissima Woodson, Ann. Missouri Bot. Gard. 26: 300. 1939.

Corollas mostly showy, white, wholly glabrous externally, the tube proper 2.5–2.8 cm long, 0.25 cm in diameter basally, gibbous, the throat narrow, ca. 2.6–2.8 cm long, densely arachnoid-villous within, the orifice ca. 0.6 cm in diameter, the lobes obliquely obovate, 2.8–3 cm long, glabrous; anthers ca. 1 cm long, glabrous; stigma with a fusiform base and digitate appendages ca. 0.3 cm long.

Known only from the type collection.

CHIRIQUI: Between Río Chiriquí & Remedios, *Woodson et al. 1179* (MO, holotype).

It is with considerable misgivings that I recognize and include this species, which is based on three corollas which Woodson collected on the ground at the base of a tall tree supporting a liana. However, he states that "complete confidence none the less may be placed in the generic identification of the corollas (which, of course, contain the stamens and stigma as is customary in the *Echitoideae*)" (Ann. Missouri Bot. Gard. 26: 300. 1939).

25. ECHITES

Echites P. Br., Civ. Nat. Hist. Jamaica 2: 182. 1756.

Lianas, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved; petioles somewhat perfoliate, glandular in the axils. *Inflorescences* dichasial, often modified by reduction or suppression, mostly axillary, 1- to many-flowered. *Flowers* small to medium-sized; bracteoles present; calyx 5-lobed, the lobes equal to subequal, bearing 1 frequently lacerate oppositely placed squamella within; corolla salverform, without appendages, the tube straight, the limb 5-lobed, the lobes dextrorsely convolute; stamens 5, included, the anthers connivent and agglutinated to the stigma, with an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries 5, separate or ± concrescent, the style 1, the stigma fusiform-subcapitate. *Fruit* apocarpous, of 2 follicles, terete, continuous or slightly articulate; seeds many, dry, rostrate, comose apically.

A genus of about seven species in Florida, Mexico, the West Indies, most of Central America, and Columbia.

Useful reference:

Woodson, R. E., Jr. *Echites*. Pp. 217–252 in "The American genera of Echitoideae." Ann. Missouri Bot. Gard. 23: 169–438. 1936.

Echites turbinata Woodson, Ann. Missouri Bot. Gard. 21: 615. 1934.—FIG. 25.

Lianas, rather stout, glabrous. *Leaves* elliptic to ovate-elliptic, shortly acuminate, obtuse to ± rounded basally, to 17 cm long and 9 cm wide, glabrous, subcoriaceous; petioles stout, ca. 1–2 cm long, with 2–3 large stipule-like glands in the axils. *Inflorescences* aggregate dichasial, axillary and alternate, several- to many-flowered, the primary peduncle 2–3 cm long. *Flowers* with the pedicels 4–8 mm long; bracteole 1(?), narrow-lanceolate, 2–3 mm long, variously placed; calyx-lobes ± equal, narrowly lanceolate, ca. 3 mm long and 0.5 mm wide, the squamella thin, lacerate marginally; corolla green to white, the tube ca. 6 mm long, pubescent within at the level of stamen attachment, the lobes ± lanceolate, 13–16 mm long; stamens attached about midway on the corolla tube, ca. 3 mm long; nectaries separate, almost as high as the ovary. *Follicles* slender, 7–8 cm long; mature seeds unknown.

Costa Rica and Panama.

CHIRIQUI: Vicinity of Casita Alta, Volcán de Chiriquí, *Woodson et al. 988* (MO). Vicinity of Cerro Punta, *Allen 1524* (MO). Río Chiriquí Viejo Valley, between El Volcán and Cerro Punta, *G. White 6* (US).

26. PRESTONIA

Prestonia R. Br., Mem. Wern. Nat. Hist. Soc. 1: 69. 1811.

Lianas, suffruticose to slightly herbaceous, lacticiferous. *Leaves* opposite, nonglandular, pinnately-nerved; petioles somewhat perfoliate, mostly glandular in the axils. *Inflorescences* ± corymbose, racemose, or umbellate, mostly axillary, rarely subterminal. *Flowers* mostly medium-sized to large; calyx 5-lobed, the lobes equal to subequal, bearing 1 or rarely several squamellae within; corolla salverform to subinfundibuliform, with or rarely without 5-epistaminal appendages, the orifice with a thickened annulus, the tube straight or gibbous, the limb 5-lobed, dextrorsely convolute; stamens 5, included or half exserted, the anthers connivent and agglutinated to the stigma, with an enlarged connective; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries 5, separate or concrescent, thin or fleshy, the style 1, the stigma fusiform or subcapitate, sometimes weakly umbraculiform below. *Fruit* ± apocarpous, sometimes connate apically or ± agglutinated, of (1–)2 follicles; seeds many, dry, comose apically.

A large genus of about 60 species mostly in northern South America, but found also in Mexico, Central America, the West Indies, and as far south as Argentina.

Useful reference:

Woodson, R. E., Jr. *Prestonia*. Pp. 276–367 *in* "The American genera of Echitoideae." Ann. Missouri Bot. Gard. 23: 169–438. 1936.

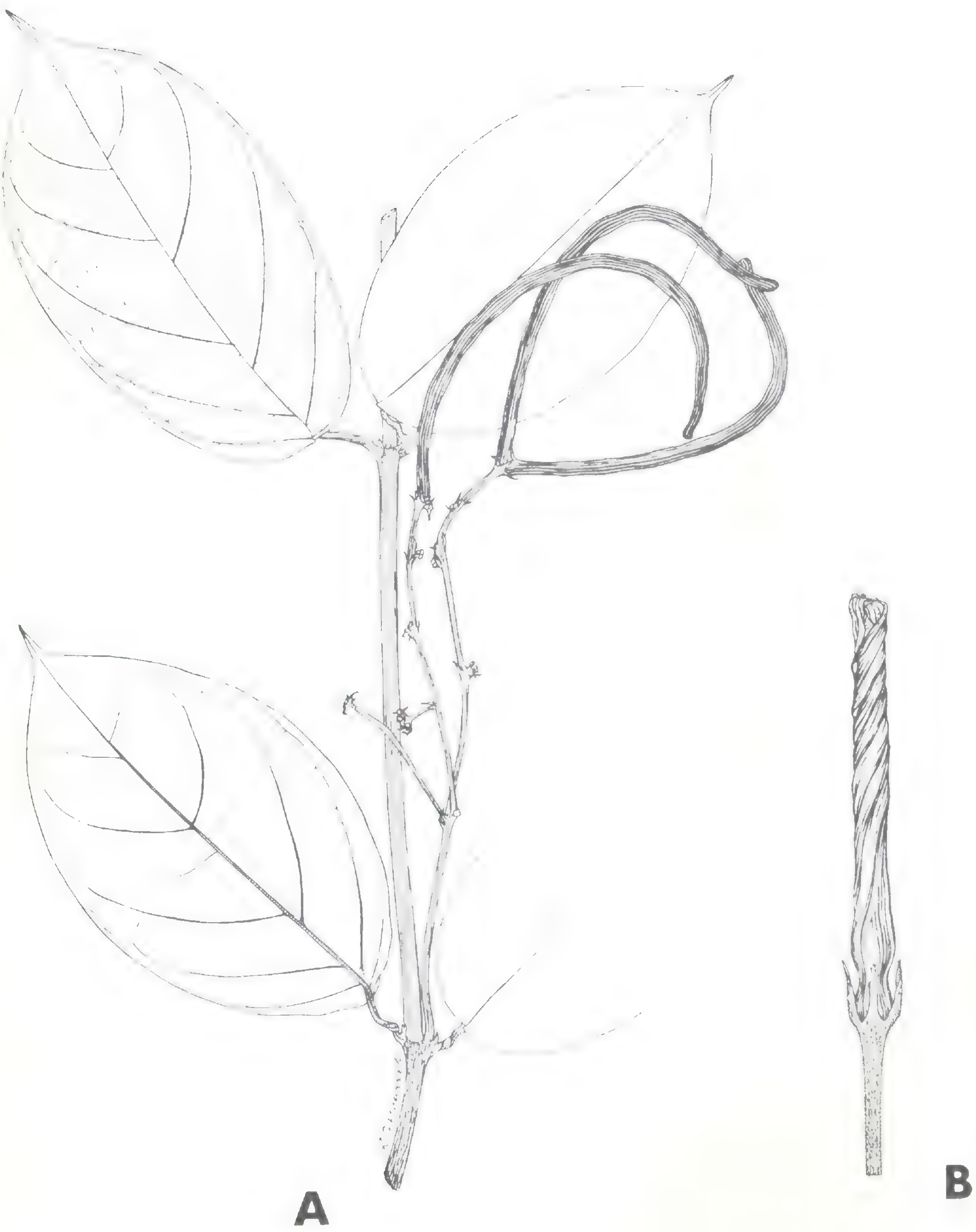

FIGURE 25. *Echites turbinata Woodson.*—A. Habit (× 3/5).—B. Flower (× 3 1/5). [After *Woodson et al.* 988 (MO).]

a. Calyx-lobes small and inconspicuous, ca. 1.5 2 mm long, ± reflexed . . . . 1. *P. acutifolia*
aa. Calyx-lobes large and conspicuous, ca. 4–25 mm long, ± erect.
b. Corolla glabrous or only papillate externally.
c. Nectaries separate, or connate only basally; calyx-lobes < 10 mm long . . . . . 2. *P. exserta*
cc. Nectaries concrescent; calyx lobes mostly > 10 mm long.
d. Nectaries thick and fleshy throughout, shorter than the ovary . . . 3. *P. obovata*
cc. Nectaries thin and ± diaphanous, at least on the margins, surpassing the ovary at anthesis . . . . . 4. *P. portobellensis*
bb. Corolla densely pubescent externally at least on the lobes.
e. Corolla-tube with elongate epistaminal appendages within; calyx-lobes 9–11 mm long . . . . . 5. *P. ipomaeifolia*
ee. Corolla-tube without elongate epistaminal appendages within; calyx-lobes mostly > 11 mm long.
f. Each calyx-lobe with a single deltoid squamella.
g. Annulus distinctly 5-lobed . . . . . 6. *P. allenii*
gg. Annulus ridged and uneven, but not distinctly 5-lobed . . . . 7. *P. wedelii*
ff. Each calyx-lobe bearing several thin calycine squamellae . . . 8. *P. remediorum*

1. **Prestonia acutifolia** (Benth.) K. Schum *in* Engler & Prantl, Nat. Pfl. 4(2): 188. 1895.

Haemadictyon acutifolium Benth. *ex* Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 167. 1860.

Lianas, the younger stems sparsely puberulent, the older lenticellate. *Leaves* elliptic, acute, obtuse basally, to 10 cm long and 3.5 cm wide, ± glabrous, firmly membranaceous; petioles ca. 3–8 mm long, weakly perfoliate, glandular in the axils. *Inflorescences* racemose, simple, the peduncle ca. 2–3 cm long. *Flowers* with the pedicals ca. 3–8 mm long, glabrous or minutely puberulent; bracteole 1, 3-lobed, ca. 0.5 mm long; calyx-lobes deltoid, ca. 1.5 mm long, bearing 1 lacerate squamella within; corolla salverform, yellow to green-yellow, the epistaminal appendages deeply included, minute, ca. 0.3 mm long, the tube 13–15 mm long, minutely puberulent externally, the lobes obliquely obovate, ca. 5–6 mm long; stamens barely exserted, the anthers ca. 4 mm long, glabrous; nectaries concrescent basally, fleshy, ca. as high as the ovary. *Follicles* unknown for Panama.

Panama and South America.

CANAL ZONE: Farfan Beach, *Tyson et. al. 3180* (MO). Around Gamboa, *Pittier 4784* (US). PANAMA: Vicinity of El Llano, *Duke 5802* (MO).

When compared with South American collections, the Panamanian material appears much more delicate.

2. **Prestonia exserta** (A. DC.) Standley, Jour. Washington Acad. Sci. 15: 460. 1925.

Haemadictyon exsertum A. DC., Prodr. 8: 426. 1844.

Vines, mostly herbaceous, the younger stems pubescent, the hairs uniseriate. *Leaves* elliptic or narrowly elliptic to obovate, acute, obtuse to shallowly rounded basally, to 10 cm long and 4.5 cm wide, pubescent, more so beneath, membranaceous; petioles 3–11 mm long, weakly perfoliate, glandular in the axils. *Inflorescences* corymbose, many-flowered, axillary and alternate, the peduncle 1–2 cm long, pubescent. *Flowers* with the pedicels 10–15 mm long, pubescent; brac-

teoles linear, ca. 2.5–3.5 mm long, pubescent; calyx-lobes narowly ovate, 6–7 mm long, bearing a squamella within; corolla salverform, green-yellow, ± glabrous externally, with 5 epistaminal appendages, the tube ca. 15 mm long, pubescent within near the level of stamen attachment, the lobes obliquely obovate, ca. 10–11 mm long; stamens half exserted, the anthers ca. 5 mm long; nectaries 5, connate basally, fleshy, as high as the ovary. *Follicles* "relatively long and slender, somewhat agglutinated when young, eventually somewhat tortuous, 23–29 cm. long, glabrous; seeds 1.2–1.3 cm. long, the pale yellowish coma 2.2–2.7 cm. long."[9]

Panama, Colombia, Venezuela, and Trinidad.

CANAL ZONE: Balboa, *Standley 32155* (US). Around Culebra, *Pittier 5723* (US). Palo Seco, *Allen 2248* (US). COCLE: Penonomé and vicinity, *Williams 362* (US). PANAMA: Bella Vista, *Killip 12009* (US). Agricultural Experiment Station at Matias Hernandez, *Pittier 6904* (US). Taboga Island, *Standley 27046* (US).

3. **Prestonia obovata** Standley, Jour. Washington Acad. Sci. 15: 459. 1925—FIG. 26A–B.

Lianas, essentially glabrous, the stems somewhat corky. *Leaves* obovate to oblong-obovate, acute, slightly rounded to obtuse basally, to 28 cm long and 13 cm wide, glabrous, coriaceous, the larger veins somewhat canaliculate; petioles to 3 cm long, stout, glandular in the axils. *Inflorescences* corymbose, usually dichotomous, the peduncle stout, to 15 cm long, shorter than the subtending leaves, the bracts apparently absent. *Flowers* with the pedicels to 4 cm long, brown-pubescent, the bracteoles variable in number, deltoid, ca. 1 mm long; calyx-lobes elongate-deltoid, sparsely to moderately pubescent, 10–15 mm long, bearing 1 squamella within; corolla salverform, yellow, sometimes with a pink or white throat, minutely papillose externally, with 5 epistaminal appendages, the tube 12–18 mm long, pubescent within at the level of stamen attachment, the lobes obliquely obovate, 12–15 mm long; stamens slightly exserted, the anthers ca. 4 mm long; ovary slightly pubescent, the nectary 5-lobed, thick and fleshy. *Follicles* weakly united, stout, ca. 25–35 cm long; seeds ca. 2–2.2 cm long, the tuft of hair ca. 3.5–4 cm long.

Apparently only from Panama.

CANAL ZONE: Near Madden Dam along Azote Caballo Road near Alahuela, *Dodge 16590* (MO). Sabanas along drowned Rio Azote Caballo, *Dodge et al. 16865* (MO). CHIRIQUI: Vicinity of San Bartolomé, Peninsula de Burica, *Woodson & Schery 869* (MO, US). DARIEN: Wooded ridge just S of El Real, *Duke 5054* (MO). 3 mi. E of Sante Fe, *Tyson et al. 4656* (MO). PANAMA: Cerro Campana, *Duke 10733* (MO). E slope of Cerro Jefe, *Tyson et al. 3337* (MO).

4. **Prestonia portobellensis** (Beurl.) Woodson, Ann. Missouri Bot. Gard. 18: 553. 1931.—FIG. 26C.

Echites portobellensis Beurl., Kongl. Svenska Vetensk. Acad. Handl. 1854: 137. 1856.
Prestonia versicolor Woodson, Ann. Missouri Bot. Gard. 23: 332. 1936.

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[9]In the absence of any fruiting material from Panama, a direct quote was taken from Woodson, Ann. Missouri Bot. Gard. 23: 300. 1936.

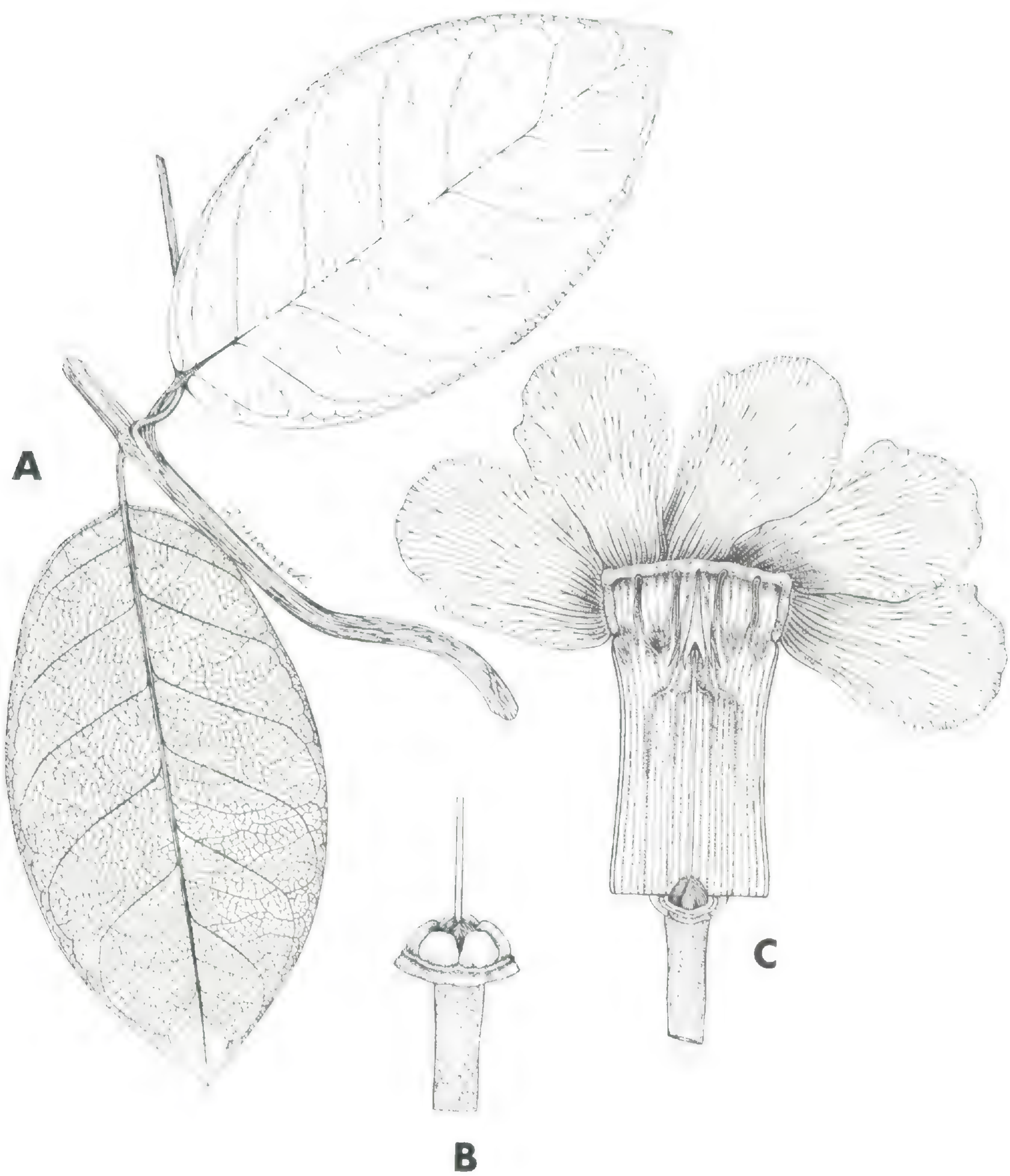

FIGURE 26. *Prestonia*.—A–B. *P. obovata* Standley.—A. Habit (× 3/10).—B. Base of flower showing thickened nectaries (× 3). [After *Tyson et al.* 3337 (MO).]—C. *P. portobellensis* (Beurl.) Woodson, dissected flower showing thin nectaries covering ovary (× 1 4/5). [After *Stern et al. 1808* (MO).]

Lianas, stout, the stems mostly glabrous, rarely pubescent. *Leaves* elliptic or oblong-elliptic to ± obovate, sometimes falcate, acute, obtuse to rounded basally, to 18(–30) cm long and 8(–15) cm wide, ± glabrous, firmly membranaceous to subcoriaceous; petioles to 2 cm long, ± perfoliate, glandular in the axils. *Inflorescences* subcorymbose, mostly di- or trichotomous, rarely simple, the peduncle ca. 2–5 cm long. *Flowers* with the pedicels 10–28 mm long; calyx-

lobes ovate to oblong-deltoid, ca. 10–13 mm long, ± tinged with purple, bearing 1 squamella within; corolla salverform, green-yellow to white, tinged with purple, with 5 epistaminal appendages, slightly exserted or reaching the orifice, the tube ca. 13–18 mm long, the lobe obliquely obovate, 10–13 mm long; stamens ca. half-exserted, the anthers 4–5 mm long, papillate dorsally; nectaries concrescent, the margins thin and diphanous, surpassing the ovary at anthesis. *Follicles* united apically at least when young, to 35 cm long, glabrous; seeds ca. 1 cm long.

Southern Mexico and Central America.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1262, 2022, 2076, 2471* (all MO). CANAL ZONE: Fort Sherman on Peña Road, *Tyson & Ah Chu 1683* (MO). CHIRIQUI: Boquete, *Davidson 684* (MO). COCLE: Vicinity of El Valle de Anton, *Allen 1800, 3552, Hunter & Allen 372* (all MO). COLON: Vicinity of Camp Pina, *Allen 3588* (MO). Cana and vicinity, *Williams 940* (NY, holotype of *Prestonia versicolor*). DARIEN: Río Balsa, between Manene and Tusijuanda, *Duke 13580* (MO). Río Chucunaque, between Río Membrillo and Río Subcuti, *Duke 8605* (MO). HERRERA: Vicinity of Las Minas, *Stern et al. 1808* (MO). PANAMA: Hills above Campana, *Allen 1887* (MO). Cerro Campana Road, trail to mountain with cross, *Kirkbride 244* (MO). San José Island, *Duke 12566, Johnston 767* (both MO). Taboga Island, *Allen 1269* (MO). SAN BLAS: Permé, *Cooper 327* (NY).

Prestonia portobellensis is a common and variable species, especially in the shape of the calyx lobes.

5. **Prestonia ipomaeifolia** A. DC., Prodr. 8: 429. 1844.

Lianas, stout, the stems generally pubescent, the hairs uniseriate, brown, ca. 1.5–2.5 mm long. *Leaves* ovate, sometimes broadly so, or elliptic to rarely obovate, acute, or sometimes acuminate, rounded and obscurely or definitely cordate basally, to 30 cm long and 14 cm wide, sparsely to densely pubescent above, mostly densely pubescent beneath, membranaceous, rarely chartaceous; petioles 2–6 cm long, generally pubescent, glandular in the axils. *Inflorescences* subumbellate, densely-flowered, the peduncle ca. 2–5 cm long, ± pubescent, bracts oblong-ovate to ± lanceolate, 7–15 mm long, pubescent. *Flowers* with the pedicels 2–9 mm long, ± pubescent; calyx-lobes ovate, 9–15 mm long, coarsely pubescent, bearing 1 lacerate squamella within; corolla salverform, yellow, densely and coarsely pubescent externally, the tube 17–18 mm long, the epistaminal appendages barely exserted or reaching the orifice, the lobes obliquely obovate, 12–14 mm long; stamens slightly exserted, the anthers ca. 5–6 mm long, glabrous; nectaries concrescent, fleshy basally, surpassing the ovary at anthesis, the stigma ± fusiform. *Follicles* stout, widely diverging, pubescent, ca. 10 cm long and 2 cm in diameter at the widest point.

Panama, Colombia, and French Guiana.

CANAL ZONE: Ancon Hill, *Duke 4583* (MO). Barro Colorado Island, *Shattuck 706* (F, MO), *Wetmore et al. 179* (F). DARIEN: Vicinity of El Real, Rio Tuira, *Stern et al. 778* (MO). Road from El Real to Pinogana, *Duke 4885* (MO). Near mouth of Rio Yapé, *Allen 366* (MO). LOS SANTOS: 0.5 mi. N of Tonosí, *Tyson et al. 3110* (MO). PANAMA: Vicinity of Bejuco, *Allen 980* (MO). Pedro Gonzalez Island, *Allen 2590* (MO). Taboga Island, *Allen 1289* (MO).

6. **Prestonia allenii** Woodson, Ann. Missouri Bot. Gard. 27: 332. 1940.

Lianas, the stems pubescent, the hairs pale-brown. *Leaves* obovate, acuminate, shallowly cordate basally, to 20 cm long and 10 cm wide, pubescent on both surfaces, densely so beneath, membranaceous; petioles ca. 5–10 mm long, glandular in the axils. *Inflorescences* umbellate, axillary, densely-flowered. *Flowers* with the pedicels to ca. 1 cm long; calyx-lobes oblong deltoid, ca. 20–25 mm long, pubescent, bearing 1 lacerate pubescent squamella within; corolla subinfundibuliform, green and white, pubescent externally, without epistaminal appendages, the annulus 5-lobed, the tube and slightly expanded throat ca. 35 mm long, the lobes obliquely obovate, ca. 15 mm long; stamens included, the anthers ca. 6–7 mm long, glabrous; nectaries concrescent, the margins thin, surpassing the ovary at anthesis. *Follicles* unknown.

Known only from the type collection.

COCLE: N rim of El Valle de Antón, *Allen & Alston 1855* (MO, holotype).

Prestonia allenii is very close to *P. wedelii*—only the structure of the annulus, ridged and unevenly lobed in *P. wedelii* versus 5-lobed in *P. allenii,* adequately separates the two taxa, and I am not fully convinced that this distinction merits specific status.

7. **Prestonia wedelii** Woodson, Ann. Missouri Bot. Gard. 29: 365. 1942.

Lianas, the stems pubescent, the hairs pale brown. *Leaves* ± elliptic, acute-acuminate, rounded to shallowly cordate basally, to 19 cm long and 10 cm wide, pubescent on both surfaces, more so on the veins beneath, chartaceous to membranaceous; petioles to 1 cm long, several gland-like stipules present. *Inflorescences* corymbose, dichotomous, axillary, the peduncles 2–3 cm long, the bracts apparently absent. *Flowers* with the pedicels 0.5–1.5 cm long, densely pubescent; bracteoles narrowly-lanceolate, ca. 1 cm long; calyx-lobes oblong-ovate, ca. 27–35 mm long, pubescent on both surfaces, bearing 1 deltoid squamella within; corolla subinfundibuliform, cream-white, pubescent externally, without epistaminal appendages, the annulus ridged and unevenly lobed, the tube ca. 20–25 mm long, the narrowly conic throat ca. 7–9 mm long; stamens included, the filaments free for 3–4 mm, the anthers ca. 3–4 mm long; nectary 5-lobed, surpassing the ovary at anthesis. *Follicles* separate, stout, pubescent, mature size unknown; seeds unknown.

Apparently only from Chiriquí Lagoon in Panama.

BOCAS DEL TORO: Chiriquí Lagoon, Water Valley, *von Wedel 1353* (MO, holotype), *1452* (MO), *1611* (MO, US).

8. **Prestonia remediorum** Woodson, Ann. Missouri Bot. Gard. 26: 299. 1939.

Lianas, the stems pubescent, the hairs pale-brown. *Leaves* ovate to obovate, shortly acuminate, cuneate to slightly rounded basally, to 18 cm long and 11 cm wide, pubescent on both surfaces, especially on the veins beneath; petioles 5–15 mm long, glandular in the axils. *Inflorescences* subcorymbose, simple, the peduncle 1.5–4 cm long, pubescent. *Flowers* with the pedicels 7–14 mm long,

pubescent; calyx-lobes oblong-ovate, ca. 16–23 mm long, pubescent, bearing several pectinate squamellae within; corolla subinfundibuliform, yellow, densely pubescent externally, the immature tube and throat ca. 2 cm long, the lobes obovate-dolabriform; anthers 7 mm long, glabrous, the apices slightly exserted; nectaries 5, concrescent at the base, fleshy. *Follicles* unknown.

Known only from Panama.

CHIRIQUI: Río Chiriquí to Remedios, *Woodson et al. 1180* (MO, holotype). COCLE: El Valle de Antón, *Seibert 493* (MO).

Both of the collections cited above had very poor flowering material, and part of the description is based on Woodson's Latin diagnosis (Ann. Missouri Bot. Gard. 26: 299–300. 1939). The specimen from Coclé had been identified as *P. ipomaeifolia* A. DC. by Woodson. However, the squamellae, pectinate and several in number, are definitely characteristic of *P. remediorum*.

27. RHABDADENIA

Rhabdadenia Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 173. 1860.

Lianas, lacticiferous. *Leaves* opposite, non-glandular, pinnately-nerved, coriaceous to membranaceous; subsessile to petiolate, the petioles somewhat perfoliate. *Inflorescences* cymose, greatly reduced, sometimes to a single flower, axillary or terminal, the bracts not apparent. *Flowers* medium-sized; calyx 5-lobed, the lobes ± equal, without squamellae; corolla infundibuliform, 5-lobed, without appendages, dextrorsely convolute; stamens 5, ± included, the anthers connivent and agglutinated to the stigma, with an enlarged connective, characterized by a tuft of hair; gynoecium 2-carpellate, apocarpous, the ovary superior, the ovules many, the nectaries 5, separate or basally connate, the style 1, the stigma fusiform. *Fruit* apocarpous, of 2 terete follicles; seeds many, comose apically.

A genus of three species in southern Florida, Mexico, Central America, the West Indies, and South America.

Useful reference:

Woodson, R. E., Jr. *Rhabdadenia.* Pp. 205–211 *in* "The American genera of Echitoideae." Ann. Missouri Bot. Gard. 23: 169–438. 1936.

Rhabdadenia biflora (Jacq.) Müll.-Arg. *in* Mart., Fl. Bras. 6(1): 175. 1860. —FIG. 27.

Echites biflora Jacq., Enum. Syst. Pl. Carib. 31. 1760.

Lianas, rarely shrub-like, glabrous. *Leaves* mostly oblong, sometimes oblong-obovate or lanceolate, mucronate, basally obtuse, to 10 cm long and 5 cm wide, glabrous, somewhat coriaceous; petioles 1–1.5(–2) cm long, mostly without glands in the axils. *Inflorescences* cymose, dichasial, reduced, 1–3(–4–5)-flowered, axillary to subterminal, the peduncles ca. 2–8 cm long, the bracts apparently absent. *Flowers* with the pedicels 5–17(–25) mm long; bracteoles minute, scarious; calyx-lobes ovate-oblong, 5–9 mm long; corolla white, sometimes with a pinkish limb, the throat yellow, the tube proper ca. 15–20 mm

FIGURE 27. *Rhabdadenia biflora* (Jacq.) Müll.-Arg.—A. Habit (× 7/10).—B. Fruit (× 7/10). [A, after *McDaniel 5145* (MO); B, after *Duke 8477* (MO).]

long, the throat conic, ca. 20–30 mm long, densely pubescent within at the level of stamen attachment, the lobes obliquely ovate, ca. 20–25 mm long and 15–20 mm wide, spreading; stamens attached at the apex of the tube proper, the anthers ca. 4 mm long, pilose apically; nectaries separate or slightly connate basally. *Follicles* slender, 10–14 cm long; seeds acicular, ca. 25–30 mm long, long-comose apically.

Southern Florida, the Greater Antilles, parts of Central America, and northern South America.

BOCAS DEL TORO: Chiriquí Lagoon, Colón Island, *von Wedel* 496 (MO). Tidal flat near Garey Creek, SE of Almirante, *McDaniel* 5145 (MO). Old Bank Island, *von Wedel* 1978 (MO). Water Valley, *von Wedel* 591, 1546 (both MO). CANAL ZONE: Barro Colorado Island, *Croat* 6574, 8296 (both MO). Chagres, *Fendler* 257 (MO). Fort San Lorenzo, *Burch et al.* 1043A (MO). Along road from Fort Sherman to Gatun, *Tyson & Blum* 3749 (MO). Near mouth of Río Chagres, *Allen* 885, *Burch et al.* 1013 (both MO). Along banks of Río Grande, *Woodson et al.* 764 (MO). CHIRIQUI: Vicinity of San Bartolomé, Peninsula de Burica, *Woodson & Schery* 933 (MO). COLON: Nuevo Chagres, beach and adjacent roadside, *Lewis et al.* 1862 (MO). DARIEN: 3 mi. E of Santa Fé, *Tyson et al.* 4670 (MO). PANAMA: Along road between Balboa & Chamé, *Dodge et al.* 16727 (MO). Vicinity of Bejuco, *Woodson et al.* 1682 (MO). Swamp between El Jagua Hunting Club on Río Jagua and El Congor Hill, *Hunter & Allen* 484 (MO). Panama Viejo, *Duke* 5759 (MO). SAN BLAS: Mainland opposite Achituppu, beach to 1.5 mi. inland, *Lewis et al.* 87 (MO). Mulatuppu, *Duke* 8477 (MO). Nargana Island, near airport, *Tyson & Duke* 1171 (MO). Soskatupu Island, *Elias* 1697 (MO).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 174. OROBANCHACEAE[1]

ROBERT R. HAYNES[2]

Herbs, often fleshy, root parasites, without chlorophyll, with 1 to many flowering stalks arising from a more or less thickened base, glabrous to pubescent with glandular or non-glandular trichomes. *Leaves* alternate, scale-like, the upper becoming bracts. *Inflorescences* racemes or spikes or rarely solitary. *Flowers* bisexual, irregular, long-pedicelled to nearly sessile, usually bracteolate, solitary in a leaf or bract axil; calyx tubular, persistent, gamosepalous, nearly regular to strongly irregular, truncate or with 1–5 teeth or lobes; corolla gamopetalous, 2-lipped, the upper lip usually 2-lobed to entire, the lower lip usually 3-lobed; stamens 4, epipetalous, alternate with the corolla lobes, didymous, the posterior stamen lacking or reduced to a staminode; anthers 2-loculed, longitudinally dehiscent; gynoecium 2–4-carpellate, the ovary superior, usually 1-loculed, with 2–4 parietal placentae, the ovules many, the style single, the stigma entire or 2–4-lobed. *Fruit* a 2–4-valved 1-loculed capsule; seeds many, small; embryo undifferentiated, the endosperm soft-fleshy and oily.

A family of about 15 genera and 140 species, widespread in both hemispheres; 1 genus, *Conopholis*, occurs in Panama. The plants have no known economic importance.

Traditionally the gynoecium of many Orobanchaceae, including the Panamanian species, has been interpreted as having two median carpels, each carpel bearing two placentae, these being displaced from the margin toward the median line of the carpel. According to this interpretation, each of the resulting four parietal placentae is the product of only one carpel. Tiagi (Vestn. Moskovsk. Univ., Ser. 6, Biol. 6: 29–52. 1962) interpreted the gynoecium of these Orobanchaceae as having four carpels, two median and two lateral, each carpel bearing two marginal placentae. According to him the placentae of adjacent carpels are fused, and thus the ovary contains four parietal placentae, each placenta being the product of two carpels.

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[1]Contribution from the Botany Program (Paper No. 778) and the Herbarium of The Ohio State University.

[2]College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210.

ANN. MISSOURI BOT. GARD. 57: 131–134. 1970.

1. CONOPHOLIS

Conopholis Wallroth, Orob. Gen. Diask. 78. 1825.

Herbs, low, glabrous to densely glandular-pubescent, cream, yellow-brown, brown, or black, simple or rarely branched, fleshy at first but becoming brittle, the flowering stems arising from a dark brown to black base. *Leaves* scale-like, sessile, with invisible to plainly evident veins, fleshy at first but becoming brittle, of 2 types, the lower tightly imbricate, short, and wide, the upper larger and scattered to somewhat imbricate. *Inflorescences* compact racemes. *Flowers* axillary to a sessile bract, the pedicels short to elongate, the bracts longer than the calyx; calyx tubular, 2-lipped, split anteriorly, 2- or 4–5-toothed or -lobed, the divisions broadly to narrowly acute or rounded, 1 or 2 subulate bractlets may arise on the base of the calyx, or these may be absent; corolla cream-colored, tubular, sometimes reflexed apically, 2-lipped, the upper lip rounded, notched, rarely 3- or 4-lobed, external in the bud, the lower lip (1–2–)3-lobed, the lobes rounded to acute; the corolla somewhat persistant, eventually ruptured and dislodged by the enlarging capsule; stamens 4(–5), the lateral 2 sometimes connate, epipetalous, inserted above the ovary, the filaments elongate, the anthers free, exserted, the locules somewhat divergent, basally attenuate, glabrous to sparingly pilose; style apically reflexed, included or exserted, persistent on or deciduous from the fruit, the stigma capitate, slightly depressed, centrally to horizontally furrowed. *Fruit* a 2-valved, 1-loculed, dull dark brown to black capsule dehiscing irregularly or anteroposteriorly; seeds oval, triangular, quadrangular, or rhomboidal with rounded or, less often, sharp angles, light to dark brown, with brown to black reticulate lines.

A genus of 2 species, both confined to the Western Hemisphere. One species with 2 varieties; 1 variety occurring in Panama.

1. **Conopholis alpina** Liebmann var. **alpina**, Forh. Skand. Naturf. Möde 4: 184. 1847.—Fig. 1.

C. panamensis Woodson, Ann. Missouri Bot. Gard. 25: 835. 1935.
C. sylvatica Liebmann, Forh. Skand. Naturf. Möde 4: 185. 1847.

Stems erect, simple, glabrous, 8–28 cm high, 6–10 mm in diameter. *Leaves* glabrous, lanceolate to narrowly elongate-triangular, (7–)12–21 mm long and 3–7(–11) mm wide, widest at or just above the base, usually sharply acute apically, the veins slightly visible to prominent; bracts glabrous, lanceolate to narrowly elongate-triangular, often concealing the calyx, 10–20 mm long and 4–6 mm wide. *Flowers* cream-colored; calyx irregularly 2- or 4–5-toothed or -lobed, the tube more or less cylindric, 3.3–4.5 mm long, split anteriorly from about half-way to all the way to the base, or not split at all, the teeth or lobes acute to rounded, 0.3–1.6 mm long; bractlets 1 or 2 or absent, 2–4.5 mm long; corolla 7.5–15.5 mm long; filaments 9–12.5 mm long, the anthers glabrous, rarely sparingly pilose, 1.6–2 mm long; style and stigma 5.5–8 mm long. *Fruit* a capsule mostly with the style and stigma deciduous, 8–16 mm long and 5–11 mm in diameter; seeds 0.4–1.7 mm long, 0.3–1.2 mm wide, and 0.3–0.8 mm thick.

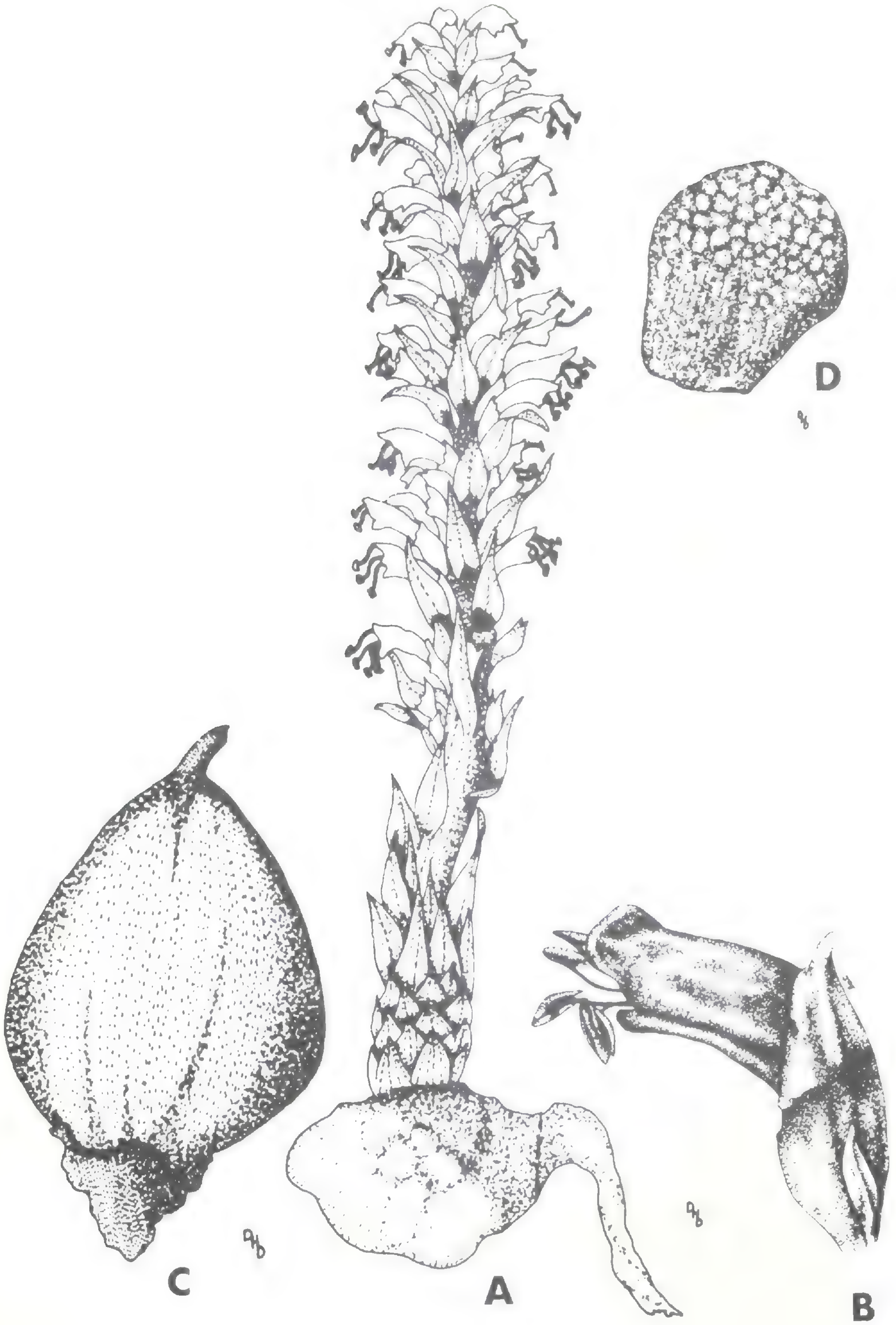

FIGURE 1. *Conopholis alpina* Liebmann var. *alpina*.—A. Habit (× 1).—B. Flower (× 5).—C. Fruit (× 4½).—D. Seed (× 300). [A–B, after *Martin 56*, Mexico (MICH); C–D, after *Allen 305* (MO).]

Under oaks in montane forests, southwest Tamaulipas south to Michoacán, Mexico, and Chiriquí, Panama. Flowering from mid-December to late April.

CHIRIQUI: Baja Chorso, Boquete District, *Davidson 399* (F, US). Trail from Bambito to Cerro Punta, *Allen 305* (MO, holotype of *C. panamensis*; F, GH, MICH, NY, UC, US, isotypes). Cerro Punto, *Lindsay 473* (F). Vicinity of Boquete, Finca Collins, *Stern et al. 2033* (ILL, MICH, MO). S of Finca Lerida, *Allen 4774* (GH). Valley of the Río Chiriquí Viejo, *White 66* (US). Valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 298* (GH). "Selva de Chango" above San Salto, Boquete Valley, *Pittier 3121* (NY, US). Volcán de Chiriquí, Boquete District, *Davidson 956* (F, GH, MO, US); vicinity of Casita Alta, *Woodson et al. 880* (GH, MO, NY); near Potrero Camp, *Killip 3604* (NY, US).

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ANNALS OF THE

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DR. GEORGE ENGELMANN: THE FIRST MAN OF CACTI AND A COMPLETE SCIENTIST[1]

OSCAR H. SOULE[2]

ABSTRACT

George Engelmann was a premier botanist in the early history of the Western United States for the half century he collected and encouraged others to collect in the region. His influence can be seen clearly through his contribution to the taxonomy of the Cactaceae where his more than 108 descriptions comprise over two-thirds of the forms recognized today.

George Engelmann was born February 2, 1809 in Frankfort-on-the-Main and died just into his seventy-sixth year in Saint Louis on February 4, 1884. His early life has been chronicled in biographies by Sargent (1884), Gray (1887), Lawton (1968), and Beidleman (1970).

By his own admission the botanical interests of Engelmann surfaced during his teenage years (Lawton, 1968) and were enhanced with his early training in Germany. The culmination of this interest appeared with his first major publication, *De Antholysi Prodromus* (Engelmann, 1832). This inaugural dissertation completed his degree of Doctor of Medicine at Würzburg in the summer of 1831. It was a morphological work based chiefly on the study of plant monstrosities and featured illustrations by the author. The care and detail shown in this early work did not go unnoticed and were a good indication of the direction and caliber of Engelmann's later work.

In 1832, Engelmann left Europe and his colleagues, including Louis Agassiz, Alexander Braun and Karl Schimper, for the United States. After landing in New York, he traveled to Philadelphia where he became acquainted with members of the scientific community. Engelmann journeyed farther west seeking a home in the reasonably unexplored region of the Mississippi Valley. Thus he arrived at Saint Louis in 1833 after a short stay in Illinois. Saint Louis was then

[1]I would like to express my appreciation to the late Dr. Edgar S. Anderson, who implanted the seed that developed into this paper. The discussions with him were stimulating to me as they have been for so many others. Acknowledgement is also given to Mrs. Carla Lange of the Missouri Botanical Garden Library for her assistance in compiling and willingness to share in the growing field of Engelmannia.

[2]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

FIGURE 1.—A landscape with *Cereus giganteus* in the region of the Gila River. The original engraving is based on a drawing by Mollhausen and first appeared in the "Cactaceae of the Boundary" (Engelmann, 1859). Since then it has been republished numerous times (Newton, 1962).

little more than a frontier trading post, but did have a small colony of resident Germans.

At this time Engelmann made a trip of approximately six months duration through southwestern Missouri, Arkansas, and western Louisiana. He intended to botanize as well as study lands, because he was under commission of an uncle in Germany who was interested in buying American land for investment and for emigration. On this trip, Engelmann caught a severe fever while in the swamps of Arkansas and was nursed back to health by a Black family. He returned to Saint Louis following his recovery and established his residence in 1835. Having used all his funds, Engelmann devoted his energy to the field of medicine. In the next few years Dr. Engelmann established a flourishing medical practice in St. Louis. He was especially popular because of his technical skill as a surgeon and physician as well as his facility with the languages—French, German, and English—of the new tri-lingual city. During his career, Engelmann introduced many innovations to the medical field in Saint Louis (Soule & Soule, 1970). Because of his early successes as a physician, Engelmann could afford to return to Germany to marry his cousin, Dora Hartsmann, on June 11, 1840, thus fulfilling a long-standing engagement. It was on the return to Saint Louis from his honeymoon that Engelmann first met Asa Gray, with whom he had been corresponding for some time. Their friendship was to stretch for almost half a century and provide much toward the development of botany in North America.

A period of ten years elapsed before Engelmann made another major botanical contribution. This was a monograph on the North American Cuscutineae which appeared in the *American Journal of Science* (Engelmann, 1842; 1843*a*), but it was soon republished in the *London Journal of Botany* (Engelmann 1843*b*), *Botanische Zeitung* (Engelmann, 1844*b*; 1846), and the *Archives de Flore* (Engelmann, 1855). This single work established an international reputation as a systematic botanist for Engelmann, one which he would permanently uphold. Correspondence with the leading names in botany from around the world resulted from this work.

Between 1832 and 1842, Engelmann made large collections of plants in the Middle West which were infrequent, if represented at all, in the herbaria of Europe. These collections he passed on freely to his German correspondents. This strengthened ties and friendships with botanical colleagues in Europe. According to Engelmann's personal files, he had 99 correspondents in foreign countries and 70 in the United States. During the period of 1835 to 1847, he sent 7,900 specimens to Berlin, 2,900 to St. Petersburg, and 900 to Asa Gray at Harvard (Tryon, 1952).

The association of Engelmann during this period as editor of a Heidleberg based journal, *Das Westland,* was short lived. Its volume in 1837 extolled the virtues of the Mississippi Valley to German emigrants and had three articles by Engelmann. In these, he gave accounts of the natural history of the region and of his near-fatal trip through Arkansas.

In 1842, Engelmann published another paper in the *American Journal of Science* in which he described several new plants from Illinois and Missouri

collected by Charles Andreas Geyer (Engelmann, 1844*a*). This further solidified Engelmann as a student of the North American flora. Geyer had collected these plants for sale to the botanical public. They were advertised by Asa Gray and could be purchased from Gray or Engelmann (McKelvey, 1955). In 1848, Engelmann with Asa Gray described the first part of a long series of plants collected in Texas by Ferdinand Lindheimer. Lindheimer, a friend of Engelmann dating back to university days in Germany, was engaged in many occupations in the Texas region and had a life-long interest in botany. At the suggestion of Engelmann around 1842, Lindheimer devoted his full time to collecting the largely unknown flora of Texas, depending on the sale of the specimens for a living (Blankinship, 1907). Engelmann urged Gray to join him and Lindheimer in the exploration of this unique flora. They took out advertisements in several botanical journals, and Lindheimer began collecting in the spring of 1843. These collections were also advertised by Hooker in the *London Journal of Botany*. Gray made many of the critical determinations; while Engelmann kept in touch with the various exploring expeditions which outfitted in Saint Louis, supplied many of the field botanists, and studied many of the most difficult genera. Upon the death of George Engelmann, his entire herbarium was presented to the Missouri Botanical Garden by his son, Dr. George J. Engelmann. In it were numerous Texas plants of Lindheimer.

George Engelmann exerted a strong influence on the botanical interests of other native Germans. For example, he encouraged August Fendler to collect plants in the Far West (Canby, 1885). He sent Fendler to Asa Gray, who got him free transportation for his baggage and collections through the Secretary of War. This took place in 1846 during the war between Mexico and the United States. Fendler got as far as Santa Fe, New Mexico. Many of these plants and Fendler's other collections eventually came to Engelmann. Engelmann's location at the "Gateway to the West" provided him with a unique opportunity to receive specimens and meet the collectors in this unexplored region. He took full advantage of this.

Another major step in building the national and international reputation of Engelmann was his description of the plants collected in the Southwest by Dr. Friedrich Adolph Wislizenus, who like Engelmann was a German physician and resident of Saint Louis. Wislizenus was in medical practice with Engelmann prior to this journey West. Later both were instrumental in the founding of the Saint Louis Medical Society. Wislizenus outfitted himself and left Saint Louis on May 4, 1846 with the hope of traveling through northern Mexico and Upper California and returning to Saint Louis in the fall of 1847. He first went to Independence, Missouri, where he joined Mr. A. Speyer, a fellow German who was heading a wagon train to Santa Fe in New Mexico. They left May 9 and arrived in Santa Fe on June 30. Even though the United States was at war with Mexico, the Mexican Governor of New Mexico treated the travelers cordially. A duty of $675 per wagon was paid, and those who wanted to go into the interior received the usual passports from the Governor. Speyer's caravan left Santa Fe July 8 for El Paso, Texas, since everything was quiet concerning the

war and they had official passports. They arrived in El Paso on the 8th of August to find some troops and cannons under General Ugarte ready to oppose the Americans. Wislizenus left the wagon train of Speyer in El Paso because of its slow pace and joined a smaller caravan of one Mr. Jacquez, a native of Chihuahua, Mexico. This group consisted of 20 Mexicans and 5 foreigners. They left El Paso on August 15 and arrived in Chihuahua City on August 24.

In Chihuahua City there was much unrest, which saw the ambitous anti-American Angel Trias take over the Governorship. By September 6 the resident Americans were evacuated by the Mexicans and on September 11 Wislizenus joined them in exile in Cosihuriachi, 90 miles west of Chihuahua City. The men were not held captive, so Wislizenus was free to collect the mountain plants near this town at 6,300 feet. After hearing on March 3, 1847 of the United States victory at Sacramento in Chihuahua, the men headed for Chihuahua City. They arrived on March 5 to meet Colonel Doniphan and his Missouri volunteers, many of whom were old friends of Wislizenus. Due to the need of a surgeon and his friendship with these men, Wislizenus joined the troops on April 5 for a trip into the southern part of Chihuahua. With no more need for Doniphan's troops in Chihuahua City, they headed for Saltillo and new orders on April 25. Outside Saltillo on May 22, General Wool ordered the troops home by way of Monterey and Matamoros. They arrived at Saltillo, the capital of Cohuila on May 23; Monterey, capital of Nuevo León on May 26, and Matamoros on June 5. The troops with Wislizenus took the steamers *Republic* and *Morillo* for New Orleans on June 10. Wislizenus arrived in New Orleans on June 17 and returned to Saint Louis in early July, completing a most remarkable and well-chronicled journey (Wislizenus, 1848). Wislizenus spent the rest of his life in Saint Louis.

The Wislizenus collection (Engelmann, 1848*b*) focused the attention of Engelman on the cacti and conifers. These two interests would remain strong in him through the remainder of his career.

Dr. Engelmann studied and described all the collections of Cactaceae which were made in the Mexican boundary region (Sargent, 1884). Even into the last year of his life, he proposed to spend considerable time in northern Mexico for the purpose of studying cacti in their native environment. This interest has resulted in George Engelmann being called "the foremost student of the Cactus family" (Benson, 1969*b*). Engelmann had started his own private garden which received contributions from all over the world. Even Prince Salm-Dyck, the noted European horticulturist, supplied numerous opuntias and other succulents in the years before 1860. Upon the death of Engelmann, much of this material was transferred to the grounds of the Missouri Botanical Garden (Cutak, 1941).

There is a conflict in the accounts of how George Engelmann was introduced to the sahuaro cactus which he was to describe *Cereus giganteus* (Fig. 1). Anderson (1969), in the description of Engelmann's early adventures, states that Engelmann was in Arizona in the early 1830's and first saw the sahuaro along the Gila River. If this is true, the precise placement of this encounter

along the Gila may be impossible without more information (Sidney B. Brinkerhoff, personal communication).

On the other hand, Asa Gray, in his biographical sketch of Engelmann (Gray, 1887), suggests that Engelmann did not venture into the Rocky Mountains, the contiguous plains in Colorado, or adjacent territories until 1880 following the death of his wife in 1879. This would be late in his life. Sargent (1884) indicates this first trip took place around 1874. If either is the case, it is possible Engelmann never saw a living sahuaro.

Engelmann states that his original description of the sahuaro (*Cereus giganteus*) is based on information and specimens provided by Lt. Col. Emory, whom he calls the first discoverer of the sahuaro (Engelmann, 1848*a*). His subsequent and more complete description (Engelmann, 1852) is based on data provided by Dr. Charles Christopher Parry, who was the botanist-geologist under the command of Emory in the spring of 1852. Parry observed the sahuaro from Tucson north to the Gila River near the present-day town of Sacaton, Pinal County, Arizona. Finally Engelmann completed his description of *Cereus giganteus* when he received information about the flowering of the sahuaro from Mr. George Thurber (Engelmann, 1854). Thurber was traveling in the region of the Gila River in the summer of 1851 and "is believed to be the only scientific gentleman who has seen the plant in question in flower" (Engelmann, 1854).

Engelmann was very cautious in his original description of the plant. He would not speculate beyond the meager notes which Emory took about its life-form. Engelmann would only say that this plant was vastly different from its nearest comparable forms and he would not comment "on the character of this species." The original sightings of the sahuaro by Emory, latitude 33° 14' 54", longitude 110° 45' 06", were along the middle part of the course of the Gila River at elevations of from 2,000 to 4,000 feet (Emory, 1848). Emory frequently refers to the sahuaro from the 1st to the 9th of November, 1846, and it appears on several plates.

The sahuaro is one of the most characteristic and easily recognized endemic plants in North America. While it was described botanically by Engelmann in 1848, the recorded history of *Cereus giganteus* goes back further.

The first sighting of the sahuaro by an Old World explorer has been attributed to Coronado around 1540 (MacDougal, 1905). Approximately a half century later Oñate provided the first printed record of this giant tree cactus (MacDougal, 1905; Britton & Rose, 1908). Later accounts such as that of Humboldt (1822: 280–281), who mentioned "cylindrical cacti which shoot up to extraordinary heights" occurring at the foot of the mountains of California, may have referred to the sahuaro (*Cereus giganteus*), the cardon (*C. pringlei*), or the hecho (*C. pecten-aboriginum*). Subsequent descriptions of the tree by Padre Juan Netwig in 1763 (Soborzo, 1966) and Pefferkorn in 1749 (Treutlain, 1949) illustrated the importance of the sahuaro to native peoples.

Descriptions of the sahuaro by explorers from eastern North America did not appear until after the first quarter of the nineteenth century. Lt. R. W. H. Hardy, Royal Navy, was among the first English speaking adventurers to note

the giant cacti of the Southwest (Hardy, 1829: 128). James O. Pattie, a trapper and Indian trader from Kentucky, referred to the sahuaro in his journal in late March of 1825 during his travels in the Gila River Valley (Pattie, 1905: 104). Both of these accounts precede the supposed discovery of *Cereus giganteus* by Lt.-Col. William H. Emory on November 1, 1846 (Sargent, 1893).

If the sahuaro is a most characteristic enemic plant, then the subtribe in which it is found, Cereinae (Hunt, 1967), is also distinctive. In the description of this group, Engelmann was without peer. He provided the names for most of the members from the arid regions of North America the organpipe cactus (*Cereus thurberi*), the senita (*Cereus schottii*), the hecho (*Cereus pecten-aboriginum*), the night blooming cereus (*Cereus greggii*), and the sahuaro (*Cereus giganteus*). The only species Engelmann did not describe are *Cereus striatus* Brandegee, a very small and physically insignificant cactus, and the cardon (*Cereus pringelei* Watson), a large columnar species for which Engelmann named two forms which have since been sunk into synonomy.

Engelmann made significant contributions to the taxonomy of other groups of cacti as well. The cactus flora of Arizona is one of the most diverse of any in the United States. Eleven genera are represented by 68 species (Benson, 1969*a*). Engelmann was involved in the description of 65% of these species, representing all eleven genera (Table 1). The contribution of Engelmann to the systematics of the Cactaceae stretches beyond Arizona. In the Southwest, for example, Engelmann named approximately 40 to 80% of all species of cacti in these states (Table 2).

TABLE 1. The Cacti of Arizona (from Benson, 1969*a*).

Genus	Total number of species	Number of species named by Engelmann
Opuntia	26	19
Cereus	5	4
Echinocereus	6	4
Mammillaria	9	6
Ferocactus	3	1
Echinocactus	2	1
Sclerocactus	2	2
Pediocactus	6	4
Epithelantha	1	1
Neolloydia	3	1
Coryphantha	5	1
Total: 11	68	44(64.7%)

In all, George Engelmann described more than 108 forms of cacti and provided the first major work on the cactus family, *Synopsis of the Cactaceae* (Engelmann, 1856). His identifications of this New World family are to be found as highly prized sheets in all the major herbaria of the world. It can be said that he had profound influence on this group and thus certainly earned the title of "the world's authority on cacti" (Anderson, 1969).

TABLE 2. Cacti of the Southwest.

Location	Number of Genera	Number of Species	Number of Species named by Engelmann (%)
Arizona (Benson, 1969a)	11	68	44 (67.7%)
California (Benson, 1969*b*)	9	34	21 (61.8%)
Colorado (Harrington, 1954)	4	21	13 (61.9%)
New Mexico (Wooton & Standley, 1915)	5	66	49 (77.5%)
Texas (Benson, 1970)	13	70	28 (40.0%)
Utah (Stanley L. Welsh, personal communication)	8	27	16 (59.3%)

Engelmann became well-known for his extremely careful and conscientious preparation. While his total output was not voluminous, it showed remarkable thoroughness. This prompted Sargent to write that "such admirable, and in these days unusual, caution has made Dr. Engelmann's botanical writings masterpieces in their way" (Sargent, 1884). In addition to the cacti other groups which received the attention of Engelmann were the euphorbias, *Juncus, Isoetes, Quercus, Abies, Juniperus, Pinus, Yucca, Agave,* and *Vitis.* His monograph on *Isoetes* was the first in North America treating a pteridophyte at the generic level, and his 1861 paper on grape damage was the first in the New World to deal with plant pathology (Ewan, 1969). The predilections of Engelmann were for the most difficult and perplexing plants. While the writings of Engelmann will be of lasting value, his name will constantly be remembered in the vegetation of the western United States through the names he provided and the taxa which commemorate him.

The photograph on the cover was made in one of the densest stands of sahuaro still in existence. It was taken March 24, 1968 in the Tucson Mountain Section of Saguaro National Monument, Pima County, Arizona. The density of sahuaro in this area can exceed fifty mature plants per acre.

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MOSSES OF TRINIDAD.
I. THE MOSSES REPORTED FOR TRINIDAD.

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ABSTRACT

A review of the literature reveals 124 mosses which have been reported for Trinidad.

Although the first collections of mosses from Trinidad apparently were made early in the nineteenth century, the various reports in the literature have never been assembled in one publication, and many collections remain to be studied and reported. This paper attempts to list, under their currently accepted names, all the mosses previously reported for the island together with references to where they were originally reported.

Müller (1849, 1851) made the first substantial contribution to the mosses of Trinidad. Based on collections distributed by Sieber and the early collections made by Crüger, Müller reported 53 species. Twenty-seven of these were described as new. Toward the end of his career Müller reported 13 species of which 10 were new (Müller, 1898). These reports were based on collections by Crüger and Broadway.

F. W. Sieber issued a few mosses from Trinidad in his exsiccata *Cryptogamia Exotica.* These were collected for Sieber by F. Wrbna in 1822 and may be the earliest moss collections made on Trinidad. In what appears to be the first record in the literature of a moss from Trinidad, Schwaegrichen (1826) reported *Macromitrium mucronifolium* based on a Wrbna collection. Although various collections from the West Indies are usually attributed to Sieber, he was never there himself. He hired Wrbna and others to collect for him and subsequently distributed the plants (Dietrich, 1881).

H. Crüger (1818–1864) probably remains the most important collector of Trinidad's mosses. Crüger was an apothecary from Hamburg who moved to Trinidad in 1841. He became director of the Royal Botanic Garden in Port-of-Spain in 1857, a post which he retained until his death (Urban, 1902). Most of Crüger's collections of mosses appear to have been made in the late 1840's.

W. E. Broadway was assistant superintendent of the Botanic Garden from 1888 until 1894, when he left to direct the botanical station on Grenada (Urban, 1902). Broadway's collections appear to be quite extensive, judging from the numbers seen in several herbaria, but most of them have never been reported in the literature. Aside from Müller's reports, the only references to these collections appear in monographic works, *e.g.*, Arzeni (1954).

In his monumental *Musci Austro-americani,* Mitten (1869) reported 74 species from Trinidad. Thirteen of these were new. Since Mitten also reported Sieber's and Crüger's mosses, he and Müller may well have reported the same

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collections under different names. With the destruction of Müller's herbarium, it may prove difficult to tie down all of these reports. However, Sieber's exsiccatae are widely distributed in European herbaria, and many of Crüger's collections exist as duplicates.

Mitten listed collections made by three of Trinidad's other early botanists. D. Lockhart founded the botanical Garden at Port-of-Spain in 1818 and remained as its superintendent until 1846 (Stearn, 1965). Lockhart was succeded by W. Purdie who was superintendent until his death in 1857. Mitten listed about twenty collections of Black. I have been unable to find any further information on Black, except his initials, J. M. (Lanjouw & Stafleu, 1954).

The remaining reports of mosses from Trinidad are scattered in a number of publications. Most of these are monographic in the broad sense of the term, but some well substantiated records are in floristic lists. The reports by Eleonora Armitage (1932), made while on a cruise to see "that marvel of engineering and efficiency," the Panama Canal, are important since they are the only records of several common mosses. While this paper appears to be only a quaint travelogue, the author did collect. At the end of the article she acknowledged the help of H. N. Dixon in determining the mosses.

William Randolph Taylor collected a few mosses during the 1939 Hancock Expedition, and these were reported by Steere (1946*a*). N. W. Simmonds collected a sizeable number of mosses during the late 1940's. Two of these proved to be new species of *Syrrhopodon* (Crum, 1956; Steere, 1946*b*), but the remaining collections have never been recorded in the literature. There are a few reports of collections by Elizabeth G. Britton, A. Fendler, and R. Thaxter. These botanists probably made rather substantial collections on the island, and these should add considerably to the number of species known from Trinidad.

In this summary of records I have included only reports which are supported by reference to specimens. Incidental mentions of a taxon occurring on Trinidad, as often encountered in regional or island floras, have not been included. Examination of the list will reveal some names which obviously require changing. I have not made these changes because I have not yet seen the appropriate specimens.

SPHAGNACEAE

Sphagnum cuspidatum Ehrh. *ex* Hoffm. var. serrulatum (Schlieph.) Schlieph. (Müller, 1849, as *S. trinitense*, sp. nov.; Mitten, 1869; Warnstorf, 1890; both as *S. trinitense;* Cardot, 1897, as *S. cuspidatum* var. *serratum* (Aust.) Aust.; Andrews, 1949.)

Sphagnum palustre L. (Warnstorf, 1891, as *S. antillarum*, sp. nov. non Besch. (1876); Cardot, 1897, as *S. cruegeri*, nom. nov. (*S. antillarum* Warnst.); Warnstorf, 1911, as *S. antillarum* Schimp. *ex* Warnst.; Andrews, 1941.

Sphagnum trinitense var. angustifolium Warnst. (Warnstorf, 1911, var. nov.)

POLYTRICHACEAE

Pogonatum tortile (Sw.) Brid. (Armitage, 1932; Frey & Duckering, 1946, as *P. convolutum* (Hedw.) P. Beauv.)

FISSIDENTACEAE

Fissidens angustifolius Sull. (Mitten, 1869; Grout, 1943.)

Fissidens kegelianus C. Müll. (Mitten, 1869; Grout, 1943.)

Fissidens leptopodus Card. (Grout, 1943.)

Fissidens littlei (Williams) Grout. (Grout, 1943.)

FISSIDENS MACROPHYLLUS Mitt. (Mitten, 1869, sp. nov.; Grout, 1943.) Grout listed this as a synonym of *F. mollis* but with the notation "in part." He did not state which of the syntypes, a Black collection and several Spruce collections, he meant.
FISSIDENS MOLLIS Mitt. (Grout, 1943.) Grout's remarks concerning *F. macrophyllus* leave doubt as to whether *F. mollis* occurs on Trinidad.
FISSIDENS PRIONODES Mont. (Grout, 1943, as *F. flexinervis* Mitt.)
FISSIDENS PSATYROCHEILON (Schlieph.) Mitt. (Schliephacke, 1855, as *Conomitrium psatyrocheilon*, sp. nov.; Mitten, 1869.)
FISSIDENS WEIRII Mitt. (Grout, 1943.)

DICRANACEAE

CAMPYLOPUS CRUEGERI (C. Müll.) Par. (Müller, 1898, as *Dicranum cruegeri*, sp. nov.)
CAMPYLOPUS PORPHYREODICTYON (C. Müll.) Mitt. (Mitten, 1869.)
DICRANELLA PERROTTII (Mont.) Mitt. (Mitten, 1869; Armitage, 1932.)
EUCAMPTODONTOPSIS PILIFERA (Mitt.) Broth. (Mitten, 1869, as *Eucamptodon piliferus*, sp. nov.; Williams, 1913*a*, as *Holomitrium p.*)
LEUCOBRYUM CRISPUM C. Müll. (Mitten, 1869.)
LEUCOBRYUM CRUEGERIANUM C. Müll. (Müller, 1898, sp. nov.)
LEUCOLOMA CRUEGERIANUM (C. Müll.) Jaeg. (Müller, 1851, as *Dicranum cruegerianum*, sp. nov.; Mitten, 1869, as *Poecilophyllum c.*; Williams, 1913*a*.)
LEUCOLOMA SERRULATUM Brid. (Mitten, 1869, as *Poecilophyllum vincentinum*, sp. nov.)
LEUCOLOMA TORTELLUM (Mitt.) Jaeg. (Mitten, 1869, as *Poecilophyllum tortellum*, sp. nov.; Williams, 1913*a*.)
MICRODUS EXIGUUS (Schwaegr.) Besch. *in* Par. (Mitten, 1869, as *Dicranella e.*)
PARALEUCOBRYUM ALBICANS (Schwaegr.) Loeske. (Mitten, 1869, as *Leucobryum megalophyllum*, sp. nov.)

CALYMPERACEAE

CALYMPERES DONNELLII Aust. (Steere, 1946*a*; Reese, 1961.)
CALYMPERES EROSUM C. Müll. (Reese, 1961.)
CALYMPERES GUILDINGII Hook. & Grev. (Müller, 1849, as *C. cruegeri*, sp. nov.; Mitten, 1869; Bescherelle, 1895; both as *C. cruegeri*; Reese, 1961.)
CALYMPERES LONCHOPYLLUM Schwaegr. (Müller, 1849; Mitten, 1869; Bescherelle, 1895, as *C. asperipes*, sp. nov.; Reese, 1961.)
CALYMPERES NICARAGUENSE Ren. & Card. (Reese, 1961.)
CALYMPERES RICHARDII C. Müll. (Reese, 1961.)
CALYMPERES ULEANUM Broth. (Reese, 1961.)
LEUCOPHANES CALYMPERATUM C. Müll. (Williams, 1920, as *L. mittenii* Card. *in* Par.)
OCTOBLEPHARUM ALBIDUM Hedw. (Armitage, 1932.)
OCTOBLEPHARUM AMPULLACEUM Mitt. (Mitten, 1869, sp. nov.; Florschütz, 1955.)
OCTOBLEPHARUM ERECTIFOLIUM Mitt. *ex* Williams. (Williams, 1913*b*, sp. nov.; Florschütz, 1955.)
SYRRHOPODON ALATOMARGINATUS Crum. (Crum, 1956, sp. nov.)
SYRRHOPODON BERTEROANUS (Brid.) C. Müll. (Müller, 1849; Mitten, 1869; Williams, 1920.)
SYRRHOPODON INCOMPLETUS Schwaegr. (Mitten, 1869, as *S. hobsonii* (Grev.) Hook & Grev.)
SYRRHOPODON LYCOPODIOIDES (Brid.) C. Müll. (Müller, 1849; Williams, 1920.)
SYRRHOPODON PARASITICUS (Brid.) Besch. *in* Par. (Müller, 1849; Mitten, 1869; both as *Calymperes disciforme* C. Müll.; Britton, 1924.)
SYRRHOPODON PROLIFER Schwaegr. (Müller, 1849, as *S. flavescens*, sp. nov.; Mitten, 1869; Williams, 1920; both as *S. flavescens*.)
SYRRHOPODON RIGIDUS Hook. & Grev. (Müller, 1849, as *S. longisetaceus*, sp. nov.; Müller, 1849; Mitten, 1869; Williams, 1920.)
SYRRHOPODON SIMMONDSII Steere. (Steere, 1946*b*, sp. nov.)

POTTIACEAE

ANOECTANGIUM EUCHLORON (Schwaegr.) Mitt. (Mitten, 1869.)
BARBULA CRUEGERI Sond. *ex* C. Müll. (Müller, 1849, sp. nov.; Mitten, 1869, as *Tortula c.*)
HYOPHILA INVOLUTA (Hook) Jaeg. (Crum & Anderson, 1958, as *H. tortula* (Schwaegr.) Hampe.)
TUERCKHEIMIA LINEARIS (Web. & Mohr) Britt. (Mitten, 1869, as *Tortula l.*)

BRYACEAE

BRYUM CRUEGERI Hampe *in* C. Müll. (Müller, 1849, sp. nov.)
BRYUM MAYNENSE Spruce *ex* Mitt. (Mitten, 1869, sp. nov.)

BARTRAMIACEAE

PHILONOTIS GLAUCESCENS (Hornsch.) Broth. (Müller, 1849; Mitten, 1869, both as *Bartramia tenella* (Brid.) C. Müll.; Dismier, 1910; Armitage, 1932.)
PHILONOTIS UNCINATA (Schwaegr.) Brid. (Müller, 1849; Mitten, 1869; both as *Bartramia berteroana* C. Müll.)

ORTHOTRICHACEAE

GROUTIELLA MUCRONIFOLIA (Hook. & Grev.) Crum & Steere. (Schwaegrichen, 1826, as *Macromitrium m.*; Müller, 1845, as *Macromitrium apiculatum* (Hook.) Schwaegr.; Müller, 1849, as *Macromitrium brevipes*, sp. nov., and as *M. mucronifolia*; Mitten, 1869, as *M. brevipes* and as *M. mucronifolia*.) See Crosby (1970*a*) for notes on the variability and nomenclature of this species.
GROUTIELLA TOMENTOSA (Hornsch. *in* Mart.) Wijk & Marg. (Steere, 1946*a*, as *Macromitrium fragile* Mitt.; Vitt & Crum, 1970.) Vitt and Crum (1970) have recently discussed this species.
MACROMITRIUM PELLUCIDUM Mitt. (Grout, 1944, 1946.)
MACROMITRIUM PERICHAETIALE (Hook. & Grev.) C. Müll. (Mitten, 1869.)
MACROMITRIUM SCOPARIUM Mitt. (Mitten, 1869, sp. nov.)
MACROMITRIUM TRINITENSE Williams. (Williams, 1921, sp. nov.; Grout, 1944, 1946.)

RACOPILACEAE

RACOPILUM TOMENTOSUM (Hedw.) Brid. (Müller, 1851, as *Hypopterygium t.*; Mitten, 1869, as *R. insigne* Hornsch. *in* C. Müll. *nom. nud.*)

LEUCODONTACEAE

LEUCODONTOPSIS GENICULATA (Mitt.) Crum & Steere. (Steere, 1946*a*, as *L. floridana* (Aust.) Britt.)
PSEUDOCRYPHAEA FLAGELLIFERA (Brid.) Britt. *in* Broth. (Mitten, 1869, as *Leucodon domingensis* (Spreng.) Mitt.)

PTEROBRYACEAE

ORTHOSTICHIDIUM PENTAGONUM (Hampe & Lor.) C. Müll. (Arzeni, 1954.)
ORTHOSTICHOPSIS AURICOSTA (C. Müll.) Broth. (Bartram, 1955.)
ORTHOSTICHOPSIS CRINITA (Sull.) Broth. (Arzeni, 1954.)
ORTHOSTICHOPSIS TETRAGONA (Hedw.) Broth. (Müller, 1851, as *Neckera quinquefaria*, sp. nov.; Mitten, 1869, as *Meteorium q.*; Arzeni, 1954.)
PIREELLA ANGUSTIFOLIA (C. Müll.) Arzeni. (Müller, 1851, as *Pilotrichum angustifolium*, sp. nov.; Mitten, 1869, as *Pterobryon a.*; Arzeni, 1954.)
PIREELLA POHLII (Schwaegr.) Card. (Müller, 1851, as *Neckera longipes* (Mont.) C. Müll.; Mitten, 1869, as *Pterobryon p.*; Arzeni, 1954.)

METEORIACEAE

METEORIOPSIS PATULA (Hedw.) Broth. (Armitage, 1932; Steere, 1946*a*.)
PAPILLARIA DEPPEI (C. Müll.) Jaeg. (Mitten, 1869, as *Meteorium d.*)
PAPILLARIA NIGRESCENS (Hedw.) Jaeg. (Müller, 1851, as *Neckera n.*; Mitten, 1869, as *Meteorium n.*; Armitage, 1932, as *P. appressa* (C. Müll.) Angstr.; Steere, 1946*a*.)

NECKERACEAE

NECKEROPSIS DISTICHA (Hedw.) Kindb. (Armitage, 1932, as *Neckera d.*)
NECKEROPSIS UNDULATA (Hedw.) Reichardt. (Armitage, 1932.)
POROTRICHUM PLICATULUM Mitt. (Mitten, 1869, sp. nov.)

HOOKERIACEAE

CALLICOSTELLA CRUEGERI (C. Müll.) Broth. (Müller, 1898, as *Hookeria cruegeri*, sp. nov.)
CALLICOSTELLA DEPRESSA (Hedw.) Jaeg. (Müller, 1851, as *Hookeria longipedunculata*, sp. nov.; Mitten, 1869, as *Hookeria l.*; Armitage, 1932, as *C. herminieri* (Schimp.) Jaeg.)

CALLICOSTELLA PALLIDA (Hornsch.) Ångstr. (Müller, 1851; Mitten, 1869; both as *Hookeria p.*)
CROSSOMITRIUM PATRISIAE (Brid.) C. Müll. (Müller, 1851, as *Hookeria p.*; Mitten, 1869, as *Lepidopilum p.*)
CYCLODICTYON ALBATUM (C. Müll.) O. Kuntze. (Müller, 1851, as *Hookeria albata,* sp. nov.; Mitten, 1869, as *Hookeria a.*)
CYCLODICTYON ALBICANS (Hedw.) O. Kuntze. (Mitten, 1869, as *Hookeria a.*)
HEMIRAGIS AUREA (Brid.) Kindb. (Mitten, 1869, as *Hookeria a.*)
HOOKERIOPSIS CRUEGERIANA (C. Müll.) Jaeg. (Müller, 1851, as *Hookeria cruegeriana,* sp. nov.; Mitten, 1869, as *Hookeria c.*
HOOKERIOPSIS CRUEGERIANA var. DIMORPHA (C. Müll.) Jaeg. Müller, 1851, var. nov.)
HOOKERIOPSIS INCURVA (Hornsch.) Broth. (Müller, 1851; Mitten, 1869; both as *Hookeria i.*)
HYPNELLA LEPTORRHYNCHA (Hook. & Grev.) Jaeg. (Müller, 1851, as *Hookeria cupressiformis,* sp. nov.; Mitten, 1869, as *Hookeria l.*)
ISODREPANIUM LENTULUM (Wils.) Britt. (Müller, 1851, as *Hookeria memberanacea,* sp. nov.; Mitten, 1869, as *Lepidopilum l.*; Müller, 1898, as *Homalia l.*; Britton & Williams, 1914.)
LEPIDOPILUM AFFINE C. Müll. (Mitten, 1869, as *L. grevilleanum* (Tayl.) Mitt.)
LEPIDOPILUM BIDUCTULOSUM (P. Beauv.) Wijk & Marg. (Muller, 1851, as *Hookeria flexifolia,* sp. nov.; Mitten, 1869, *Lepidopilum f.*)
LEPIDOPILUM INTERMEDIUM (C. Müll.) Mitt. (Müller, 1851, as *Hookeria intermedia,* sp. nov.; Mitten, 1869.)
LEPIDOPILUM LATIFOLUM (C. Müll.) Mitt. (Müller, 1851, as *Hookeria latifolia,* sp. nov.; Mitten, 1869.)
LEPIDOPILUM POLYTRICHOIDES (Hedw.) Brid. (Müller, 1851, as *Hookeria p.*; Mitten, 1869.)
LESKEODON AURATUS (C. Müll.) Broth. (Muller, 1851, as *Mniadelphus auratus,* sp. nov.; Mitten, 1869, as *Disticholphyllum a.*)
NEOHYPNELLA DIVERSIFOLIA (Mitt.) Welch & Crum. (Müller, 1898, as *Hookeria chrysophyllopodia,* sp. nov.; Welch & Crum, 1959.)
PILOTRICHIDIUM CALLICOSTATUM (C. Müll.) Jaeg. (Müller, 1851, as *Hookeria callicostata,* sp. nov.; Mitten, 1869; Müller, 1898; both as *Hookeria c.*
PILOTRICHUM ANDERSONII Crosby. (? Müller, 1851, as *P. bipinnatum* var. *filinerve,* var. nov.; Crosby, 1969, sp. nov.)
PILOTRICHUM BIPINNATUM (Schwaegr.) Brid. (Müller, 1851; Mitten, 1869; Crosby, 1969.)
PILOTRICHUM EVANESCENS (C. Müll.) Crosby. (Müller, 1851, as *P. bipinnatum* var. *e.*; Mitten 1869, as *P. trinitense,* sp. nov.; Crosby, 1969.)

LEUCOMIACEAE

LEUCOMIUM COMPRESSUM Mitt. (Mitten, 1869, sp. nov.)

THUIDIACEAE

THUIDIUM COMPLANUM Mitt. (Mitten, 1869, sp. nov.)
THUIDIUM INVOLVENS (Hedw.) Mitt. (Müller, 1851, as *Hypnum i.*)
THUIDIUM RECOGNITUM (Hedw.) Lindb. var. DELICATULUM (Hedw.) Warnst. (Müller, 1851, as *Hypnum d.*)

BRACHYTHECIACEAE

LEPYRODONTOPSIS TRICHOPHYLLA (Hedw.) Broth. (Müller, 1851, as *Neckera t.*; Mitten, 1869, as *Lepyrodon t.*)

PLAGIOTHECIACEAE

PILOSIUM CHLOROPHYLLUM (Hornsch.) C. Müll. *in* Broth. (Müller, 1851, as *Hypnum c.*; Mitten, 1869, as *Stereophyllum c.*)
STEREOPHYLLUM LEUCOSTEGUM (Brid.) Mitt. (Müller, 1898, as *S. leucothallum,* sp. nov.)
STEREOPHYLLUM LEUCOTHALLUM var. ADREPENS C. Müll. (Müller, 1898, var. nov.)

SEMATOPHYLLACEAE

ACROPORIUM PUNGENS (Hedw.) Broth. (Müller, 1851, as *Hypnum p.*)
APTYCHUS FLACCIDIFOLIUS C. Müll. (Müller, 1898, sp. nov.)

MEIOTHECIUM BORYANUM (C. Müll.) Mitt. (Mitten, 1869.)
PTEROGONIDIUM PULCHELLUM (Hook.) C. Müll. *in* Broth. (Mitten, 1869, as *Potamium p.*)
SEMATOPHYLLUM CAESPITOSUM (Hedw.) Mitt. (Müller, 1851, as *Hypnum kegelianum* (C. Müll.) C. Müll. and as *Hypnum c.*)
SEMATOPHYLLUM FLACCIDIFOLIUM (C. Müll.) Mitt. (Müller, 1851, as *Hypnum flaccidifolium*, sp. nov.; Mitten, 1869.)
SEMATOPHYLLUM SUBSIMPLEX (Hedw.) Mitt. (Müller, 1851, as *Hypnum s.*; Mitten, 1869.)
TAXICAULIS CHALAROPHYLLUS C. Müll. (Müller, 1898, sp. nov.)
TAXITHELIUM PLANUM (Brid.) Mitt. (Mitten, 1869; Müller, 1898, as *Sigmatella p.*)
TAXITHELIUM PLANUM var. FLAVESCENS (C. Müll.) Par. (Müller, 1851, as *Hypnum planum* var. *flavescens*, var. nov.)
TRICHOSTELEUM APIOCARPUM (Mitt.) Jaeg. (Mitten, 1869, as *Sematophyllum apiocarpum*, sp. nov.)

HYPNACEAE

ISOPTERYGIUM ARANEOSETUM (C. Müll.) Par. (Müller, 1898, as *Taxicaulis araneosetus*, sp. nov.)
ISOPTERYGIUM TENERUM (Sw.) Mitt. (Mitten, 1869.)
MITTENOTHAMNIUM DIMINUTIVUM (Hampe) Britt. (Mitten, 1869, as *M. thelistegum* (C. Müll.) Mitt.)
RHACOPILOPSIS TRINITENSIS (C. Müll.) Britt. & Dix. (Müller, 1851, as *Hypnum trinitense*, sp. nov.; Mitten, 1869, as *Ectropothecium t.*)
VESICULARIA AMPHIBOLA (Spruce *ex* Mitt.) Broth. (Mitten, 1869, as *Ectropothecium amphibolum*, sp. nov.)
VESICULARIA CRUEGERI C. Müll. (Müller, 1898, sp. nov.)
VESICULARIA SUBDENTICULATA (C. Müll.) Broth. (Müller, 1851, as *Hypnum subdenticulatum*, sp. nov.; Mitten, 1869, as *Ectropothecium s.*)

EXCLUDED SPECIES

PILOTRICHIDIUM DIATOMOPHILUM (C. Müll.) Crosby. (Müller, 1898, as *Hookeria diatomophila*, sp. nov.) This species is based on a Charles Wright collection. Müller (1898: 247) decribed it from "Insula Trinidad Antillarum," but this was corrected, in the same paper, to "Cuba prope Trinidad" (Müller, 1898: 266). Subsequent authors have overlooked this correction, and this species is still attributed to Trinidad (Fleischer, 1922; Wijk *et al.*, 1959). See Crosby (1970*b*).

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THE FLOWERS OF *TRATTINNICKIA ASPERA* (BURSERACEAE) DISCOVERED

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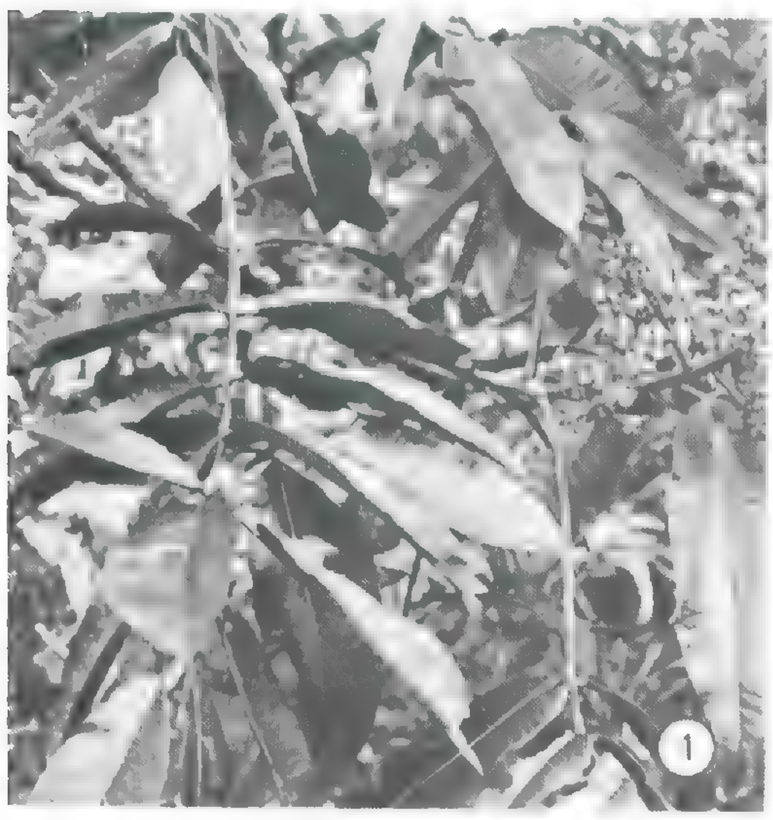
ABSTRACT

The first published description is given for the flowers of *Trattinnickia aspera,* endemic to Panama.

Although Swart (1942: 426) wrote of *Trattinnickia aspera* (Stanley) Swart as having "flowers 3-merous," flowering specimens of this Panamanian endemic tree heretofore apparently have never been collected. All exsiccatae cited by Swart in his monograph [*Standley 40815* (US); *Standley 41161* (US, holotype; US, isotype)] have been examined by the junior author. None proved to be in flower; *Standley 40815* is sterile, and *Standley 41161* is fruiting. All other collections of this species seen from F, GH, MO, and US, likewise, have been sterile or in fruit. Consequently, the description of *Trattinnickia aspera* given in the *Flora of Panama* (Porter, 1970) lacks floral characters.



FIGURES 1 2.—*Trattinnickia aspera* (Standley) Swart. 1. One branch showing part of terminal staminate inflorescence, × 1/10.—2. Staminate inflorescence, × ¼. [*Croat 11667.*]

While the treatment for the Burseraceae of Panama was in press, the senior author collected flowering specimens from both staminate and carpellate trees on Barro Colorado Island. The following description of the inflorescence and flowers of *T. aspera* is based on these collections [CANAL ZONE: Barro Colorado Island, Armour Trail, 1040, 40 m north, *Croat 11667* ♂ (MO, SCZ); Snyder-Molino Trail, 300, 30 m north, *Croat 11881* ♀ (MO, SCZ)] The description is based on both fresh and dried specimens.

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ANN. MISSOURI BOT. GARD. 57: 152–154. 1970.

Inflorescence terminal, paniculate, usually pinnately branched, occasionally bipinnately branched, to 29 cm long, hispidulous, the lower part of the main axis with thin brown periderm (often flaking in dried specimens); branches few to many, to 11 cm long, sharply angulate, densely floriferous; flowers dull red (occasionally only partly so in carpellate flowers), densely puberulent and obscurely glandular dotted, glomerulate on branches, at least the staminate flowers in various stages of development; pedicels to 4 mm long at anthesis, accrescent in fruit, broadened apically, distinctly flattened, often drying with 3 edges; calyx sericeous within, ca. 2.7 mm long, with 3 valvate lobes in bud, falling soon after opening (before corolla is fully expanded); staminate corolla somewhat urceolate, mostly glabrous within, 4.3–5.3 mm long and 3.3–4.3 mm wide, 3-lobed, the lobes acute, usually divided less than ½ way to the base, erect or somewhat spreading; stamens usually 6 (rarely 10, then smaller with more distinct filaments), almost sessile, the filaments strap-shaped, the anthers oblong, to 2 mm long and 1 mm wide, introrse, longitudinally dehiscent; ovary

FIGURE 3.—*Trattinnickia aspera* (Standley) Swart, close up of staminate flowers, × 1¼. [*Croat* 11667.]

conical, shorter than the stamens, vertically grooved to the apex, the styles 2, slender and minute, appressed together; carpellate corolla of similar size and shape as the staminate but perhaps less brightly colored, occasionally with tinges of green, lobed ¼ to ¾ way to the base; stamens 6, abortive, oblong, 0.7–0.9 mm long and ca. twice as long as broad, essentially sessile, inserted on the rim of the rather prominent disk; ovary more or less ovoid, glabrous, smooth and

shiny (at least in fresh specimens), 2–2.7 mm long at anthesis, the styles 2, short and thick, closely appressed together and appearing as a simple 2-lobed unit.

Original observations based on a few fallen dried flowers showed them to contain 5, 6, and 10 stamens. However, after climbing the tree for an adequate sampling of fresh flowers, the numbers 5 and 10 were never repeated despite the fact that numerous flowers were observed. The 10-staminate condition is probably quite rare, and the 5-staminate count was possibly the result of an imperfect specimen.

Because of the differences in stamen size and the condition of the ovary, the sex of any tree can easily be determined in the field by the examination of fallen flowers. Staminate flowers usually fall from the tree after the pollen has been shed, in most cases with the corolla still attached.

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A NEW SPECIES OF *DICRANOSTYLES* (CONVOLVULACEAE) FROM VENEZUELA

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ABSTRACT

A new species of *Dicranostyles*, *D. costanensis*, is described from the Costal Cordillera and lowland forests of Apure State, Venezuela. The collections of this species extend the known range of the genus northwest of the llanos.

At the Instituto Botanico in 1967 we discussed collections of a new species of *Dicranostyles* from the cloud forests of the Venezuelan Coastal Cordillera. Because the junior author had been studying that genus and the related genera *Lysiostyles* and *Maripa*, it was decided that we would publish the new Venezuelan species together. The collections of *D. costanensis* are the first made from northern and northwestern Venezuela and extend the range of the genus north of the South American llanos.

Dicranostyles costanensis Steyermark & Austin, sp. nov.

A *D. scandenti* affinis et cum ea ovario glabro, sed thyrsis longioribus, tomento densiore et magis cinnamomeo vel castaneo, floribus densioribus, foliis basis obtusis vel subrotundatis, corollis et stylis longioribus, et distributus in et circa montibus costanensis Venezuelis differt. Etiam similibus a *D. ampla* var. *ampla*, sed ovario pubescenti et regna Amazona habitat distincta est.

Lianas; stems gray-red to reddish-brown, smooth, with white lenticels. *Leaves* with petioles 12–20 mm long; blades oblong, elliptic-oblong to ovate, 4–9 (–12) cm long and 3–5 cm wide, the base subrotund to obtuse, the apex acuminate, thinly coriaceous, the secondaries 8–13 pairs; glabrescent on both sides. *Inflorescences* axillary, aphyllothyrsiform, 4–18 cm long, densely cinnamon-brown pubescent; bracts 1–2 mm long, oblong, acute, pubescent. *Flowers* with pedicels ca. 1 mm long; sepals deltoid-suborbiculate, obtuse, 1.5 mm long and 1.9–2 mm wide, pubescent without, glabrous within, margins ciliolate with non-glandular trichomes; corolla subrotate, white, ca. 5 mm long and ca. 5 mm wide, the tube short, ca. 1.2 mm long, ca. 2 mm wide at summit, ca. 1.5 mm wide at base, glabrous without, the lobes elliptic-oblong, thickened and subinflexed at the acute apex, ca. 3.5 mm long and ca. 1.8–1.9 mm wide, pubescent without, glabrous within; stamens excluded, the filaments ca. 3 mm long, inserted ca. 1 mm above corolla base, basally glandular pubescent, the anthers ca. 1 mm long, oblong, basally sagittate; ovary conic-oblong, ca. 1 mm long and ca. 0.5 mm in diameter, glabrous, the styles 2, free for 0.5–1.5 mm, mostly united in basal 0.3–0.7 mm, total length ca. 2 mm, glabrous, the stigmas capitate to ± complanate and irregularly lobed. *Fruits* ellipsoid, 22–25 mm long and 17–19 mm in diameter, striae

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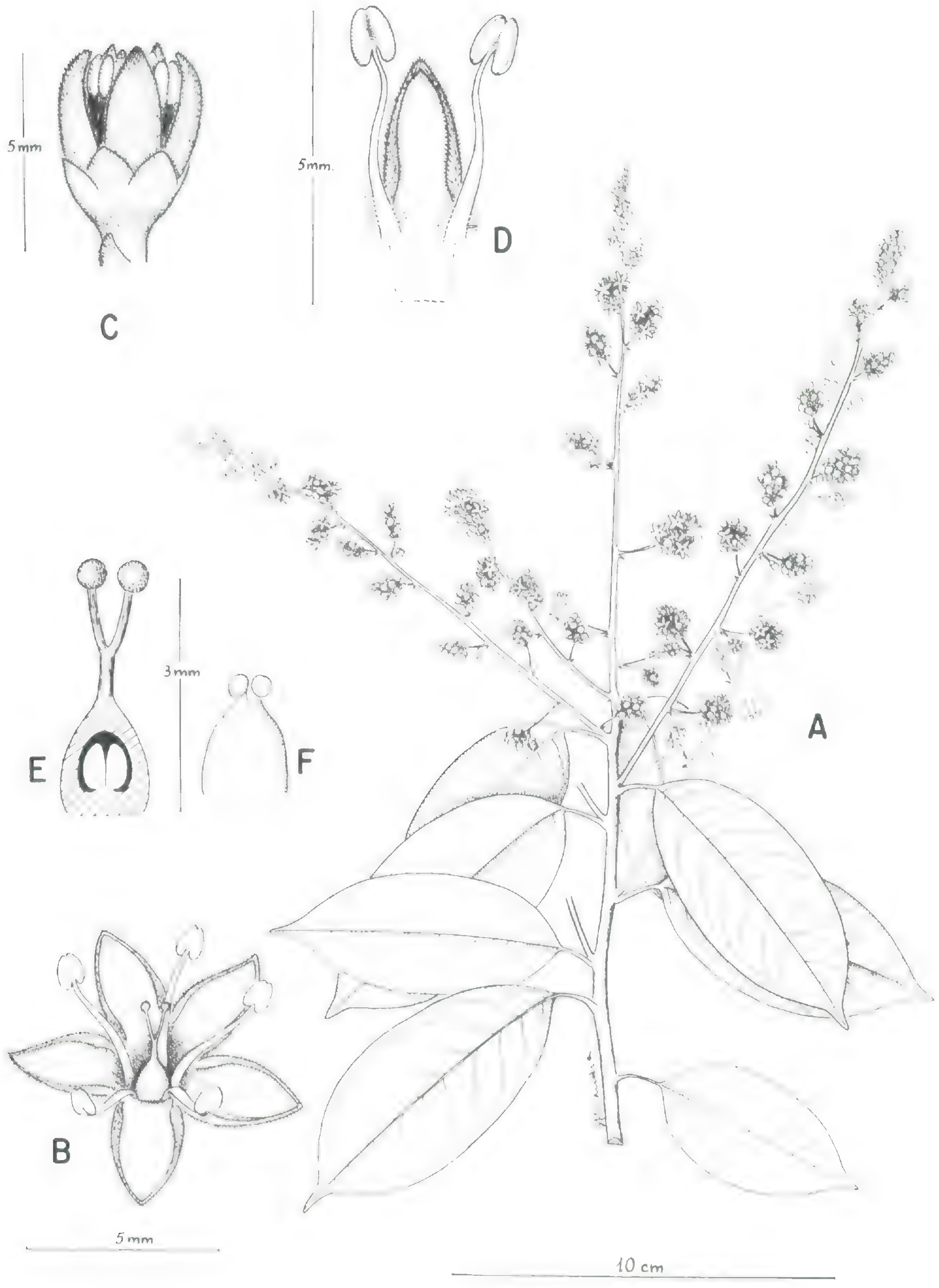

FIGURE 1. *Dicranostyles costanensis*—A. Habit.—B. Flower.—C. Bud before complete anthesis.—D. Detail of stamens and attachment.—E. Detail of gynoecium.—F. Detail of immature gynoecium dissected from bud. [After *Steyermark et al. 100263* (VEN).]

obscure, somewhat shiny, brown to dark brown, calyx reflexed to ca. 180°; seed 1, ellipsoid, ca. 15 mm long and ca. 13 mm in diameter.—Fig. 1.

Holotype: VENEZUELA. YARACUY: Cerro La Chapa, selva nublada al norte de Nirgua, on ridge leading to Quebrada de Camburito, altitude 1200–1400 m, *Steyermark, Bunting & Wessels-Boer 100263* (VEN).

Coastal Cordillera in cloud forests from 1200–1500 m, and in the lowlands of the state of Apure from 250–280 m. Flowering March, April, and November; fruiting November.

VENEZUELA. APURE: Reserva Forestal San Camilo, selva seimpreverde a lo largo de la Quebrada La Azuilita, al suroeste del caserio San Camilo (El Nula), altitude 280 m, *Steyermark, Bunting & Blanco 101634* (VEN). Reserva San Camilo, a lo largo de la Quebrada de la Cristalina hasta la vega del Cerro La Nulita, altitude 250 280 m, *Steyermark, Bunting & Blanco 101732* (VEN). ARAGUA: Selvas de la Mesa, Parque Nacional, liana, altitude 1400 m, *Pittier & Nakichenovich 14447* (VEN). DISTRITO FEDERAL: Cerro Naiguata, laderas pendientes del lado del mar que miran hacia al norte, arriba del pueblo de Naiguata, bosque humedo denso, Lomas de Las Delicias, entre Quebrada de Basenilla y Quebrada Guayoyo, 9 12 km SW de Hacienda Cocuizal, altitude 1390 1500 m, *Steyermark 91953* (MO, VEN).

Dicranostyles costanensis in a member of the difficult *D. scandens* complex. Members of this complex are much less distinct than any others in the genus, and the five taxa involved vary in subtle but reasonably consistent characters. Ovary pubescence, leaf shape, and color of the inflorescence indument are primary characters for determination. The few collections of this complex which are now available suggest that three species (*D. ampla, D. costanensis,* and *D. scandens*) are involved. *Dicranostyles ampla* has three varieties.

Collections further indicate that the genus *Dicranostyles* is a rare member of the South American lowlands. Only about 106 collections are known for the fifteen species. Four species are known from only the type collection, three from only two collections, and only six of the fifteen from five collections or more. More collections are needed to better understand the interspecific relations.

THE LICHEN FAMILY HEPPIACEAE IN NORTH AMERICA[1]

CLIFFORD M. WETMORE[2]

ABSTRACT

This paper is a monographic treatment of the Heppiaceae in continental North America north of Mexico and treats 13 species and 3 varieties. The family occurs mainly in arid areas and is very abundant in parts of the southwestern United States. Culture experiments on the phycobionts and whole lichens are described. Only one lichen substance is reported from the family. This unknown substance occurs in the epithecium and gives a red-violet reaction with KOH and nitric acid. Two genera are recognized—*Heppia,* with one species (*H. lutosa*), and *Peltula* (including *Heterina*). The genus *Heppia* is separated from *Peltula* on the basis of the number of spores per ascus, the gelatinous sheath on the ascus, and the phycobiont.

New combinations made are *Peltula bolanderi* (Ach.) Wetm., *P. clavata* (Kremp.) Wetm., *P. euploca* (Ach.) Wetm., *P. michoacanensis* (B. de Lesd.) Wetm., *P. obscurans* var. *deserticola* (Zahlbr.) Wetm., *P. obscurans* var. *hassei* (Zahlbr.) Wetm., *P. omphaliza* (Nyl. *in* Eckf.) Wetm., *P. placodizans* (Zahlbr.) Wetm., *P. polyspora* (Tuck.) Wetm., *P. tortuosa* (Nees) Wetm., and *P. zahlbruckneri* (Hasse) Wetm. *Peltula cylindrica* from Georgia is described as new. True *P. tortuosa* is reported from the United States for the first time. Keys, photographs, and maps given for the taxa included along with descriptions and citations of specimens seen.

This paper hopefully begins a series of extensive continental revisions of the lichen family Heppiaceae. The area covered in this study includes all of North America north of Mexico, except Greenland. The Caribbean islands will be included with Mexico in a later paper.

Modern collections are especially necessary for revisions of poorly known families such as this. The Heppiaceae has been somewhat neglected by collectors, because most North American botanists have collected in the summers and few wanted to spend any more time than necessary in the hot deserts. Also, since most of the species are small and easily overlooked, one must actually get down on hands and knees when looking for Heppiaceae. Additional collections were required to give a better idea of total distributions of most of the species, to obtain more adequate material for study, and to observe variation in the field. Three extensive collecting trips were made to find Heppiaceae. The first covered the central and northern Great Plains; the second covered the southern part of the Great Plains west to California; and the third covered the area in between. These three trips covered about 16,500 miles. Over 4,000 lichens were collected, including about 300 of Heppiaceae. All lichen taxa seen at each locality were collected to guard against missing some Heppiaceae and to provide more collections of lichens from arid parts of the United States for other distributional studies.

[1]I acknowledge the receipt of National Science Foundation Grant GB-4812 which made this study possible. I wish to thank the curators of the herbaria for lending collections for this study and to acknowledge the assistance of numerous people in connection with the field work. Wartburg College has made contributions toward the completion of this study and this assistance is greatly appreciated.

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In preparing terricolous lichens for the herbarium it is often advisable to glue the soil to prevent crumbling and loss of the specimen. In the Heppiaceae this is an absolute necessity, and even before shipment from the field to the laboratory all terricolous material obtained on these trips was so treated. However, care must be taken so that glue does not soak into the thallus.

History

Of the species now included in the Heppiaceae, the first described was *Lichen euplocus* Ach. in 1798, but this epithet was not brought into the Heppiaceae until 1921. The genus *Heppia* was described by Naegeli *in* Hepp in 1853 with *H. urceolata* Naeg. *in* Hepp as the type species. In 1853 Nylander described the genus *Peltula* with the type species *P. radicata,* but this generic name was not used again until much later.

By 1890 there were numerous species which Wainio (1890) grouped into the tribe Heppieae. In his Brasilian material he recognized one genus, *Heppia,* and divided it into section *Heterina* with two species, section *Pannariella* with two species, and section *Solorinaria* with two species. Zahlbruckner (1907) was the first to recognize the Heppiaceae as a family and included one genus, *Heppia,* with four sections and 40 species. Zahlbruckner (1922–40) lists 94 taxa in the family, and more have been added since.

The first attempt to revise the species of the family was by Hue (1907). He studied and described 23 species and listed 55 more of which he had seen no specimens. Gyelnik (1935) revised the European taxa and described or recognized many small genera within the family. No other revisionary treatment has been attempted, although Harmand (1913) and Hasse (1913) studied the taxa in their areas in some detail.

The first taxon of the family reported from North America was *Heppia despreauxii* reported by Tuckerman *in* Lea (1849) followed by *H. holanderi* and *H. guepinii* (Tuckerman, 1872). Zahlbruckner described several species, sent to him by Hasse from the western United States, and Bouly de Lesdain described additional taxa from North America, so that today there have been 24 taxa reported from the United States.

Few collectors have collected specimens of Heppiaceae in North America. The outstanding collector was Hasse, who made many collections of the family in southern California, where most of the species occur. These lichens grow in places collectors usually like to skip during summer trips and are small and inconspicuous so they are easily overlooked. It is not surprising that their great abundance has been missed.

Morphology and Anatomy

Most anatomical studies were made on freehand sections. For best results sections of the medulla and cortex should not be over 10–20μ thick. Additional sections were made with a freezing microtome for permanent slides. All tissue measurements were made in water, and other measurements were made in KOH.

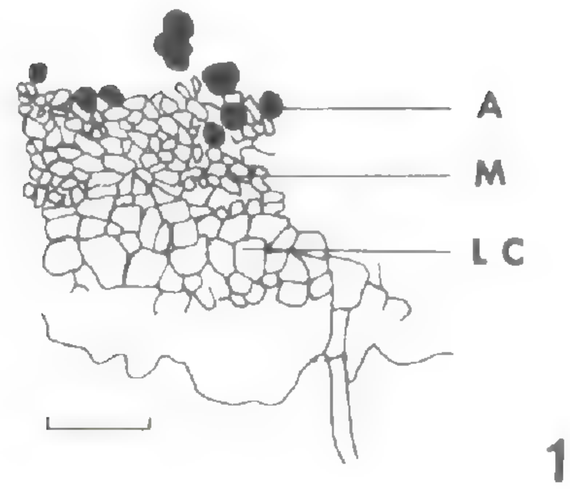
The thallus in the Heppiaceae is mainly squamulose, but in some species it may become areolate or subfruticose. The thallus in *Heppia lutosa* is of flat

squamules which are broadly attached by hyphae. The squamules are more or less roundish and are variable in size from 1–7 mm. In the genus *Peltula* the thallus is areolate, squamulose, peltate, or subfruticose with the thallus units attached at one point. The thallus is more or less roundish and flat to convex and varies from 0.5 mm in diameter in *P. obscurans* var. *deserticola* to 10 mm in diameter in *P. euploca*. In some species the thallus can become deeply lobed and polyphyllous. The attachment is by numerous, large rhizoids or a single umbilicus which may branch at the point of attachment to the substrate. *Peltula placodizans* has an almost areolate thallus in the center but more or less elongated, prostrate, placodiform lobes at the edge. In *Heterina* the thallus is subfruticose and the lobes are terete or flattened and up to 10 mm long and 1 mm thick. The attachment is by a simple umbilicus with one to several lobes attached and ascending from one umbilicus. The umbilicus in *Peltula* may sometimes continue to grow after the main thallus has been broken off. Several times collections of *P. euploca* on rock were seen with additional growth from a naked umbilicus, however, none was seen to redevelop the peltate main thallus.

Soralia are present in three North American species and are either marginal or laminal. In *Peltula bolanderi* the soralia are mainly marginal, while in *P. euploca* the soralia are both marginal and laminal. The soredia are farinose and quite compact in the soralia. In *P. placodizans* soredia are in capitate mounds on the areoles.

Members of the Heppiaceae have a heteromerous thallus with a more or less distinct medulla. A cellular cortex is usually well developed on the lower surface of the thallus and is of the paraplectenchymatous type (Fig. 1). The upper surface rarely has a cortex of any sort but is covered with a thin necral layer. *Heppia lutosa* is paraplectenchymatous throughout, but *Peltula clavata* and *P. richardsii* have no cortices at all. In some cases the lower cortex has cells of different shape or size than the medulla (Fig. 1). But in other cases (*Heppia lutosa, Peltula obscurans* var. *obscurans,* and *P. placodizans*) the cells are the same as in the cellular medulla.

The medulla is either paraplectenchymatous or of loose hyphae and can vary from about half of the thallus thickness to almost none. In *Heppia lutosa, Peltula polyspora,* and *P. placodizans* there is a continuous paraplectenchymatous medulla (Fig. 1), but in *P. michoacanensis* the medulla is sometimes cellular and sometimes of agglutinate hyphae. To determine the type of medulla very thin sections are necessary. In *Peltula obscurans* the medulla varies from usually cellular in var. *hassei* and var. *obscurans* to usually loose hyphae in var. *deserticola*. The medulla type in *P. obscurans* can vary even within the same thallus lobe from completely cellular to mostly loose with a few cellular areas. In var. *deserticola* and var. *hassei* this seems to be correlated with the pH of the substrate—on calcareous substrates there is less development of cellular tissue in the medulla and lower cortex, but on acid substrates there is better development. A medulla of loose hyphae (Fig. 2) is found in *P. bolanderi, P. euploca, P. richardsii,* and *P. omphaliza*. In *P. zahlbruckneri* and *P. cylindrica*



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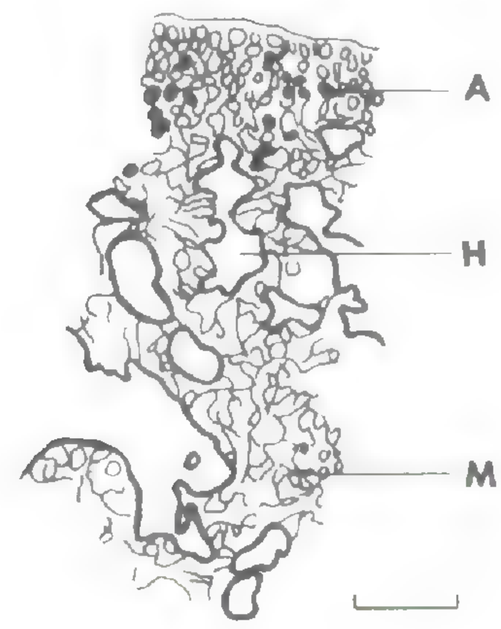

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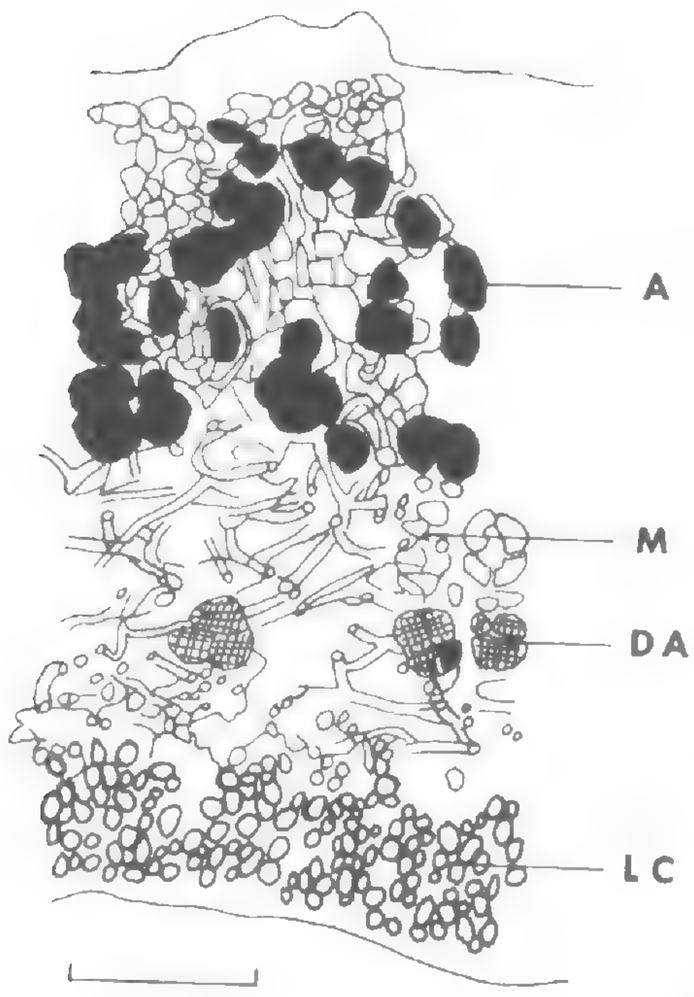

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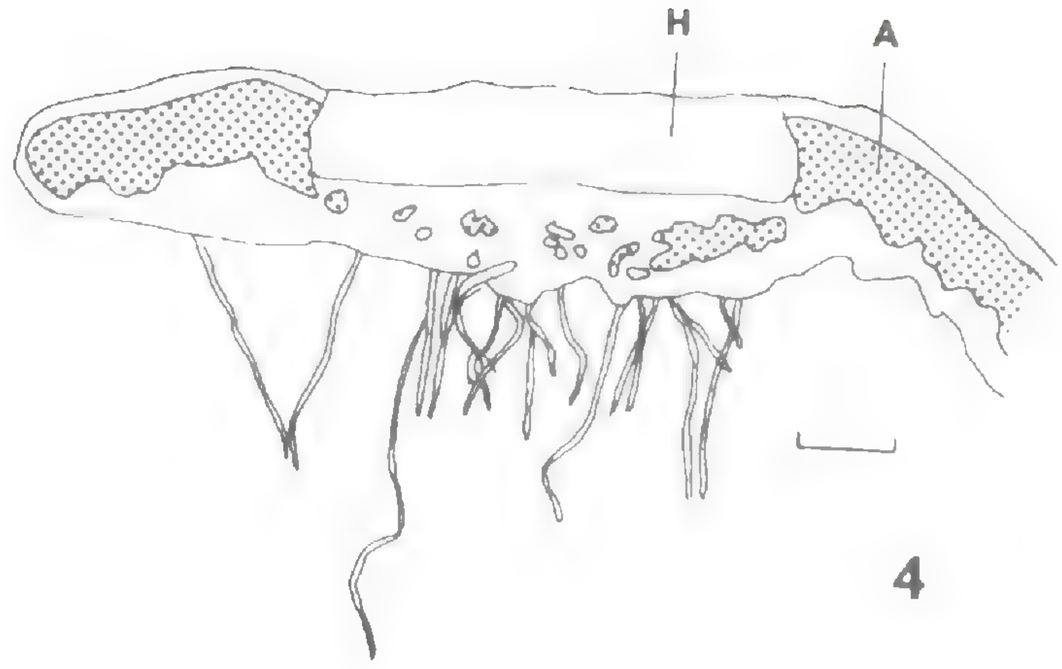

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FIGURES 1–4. Anatomy of North American Heppiaceae.—1. Lower cortex and cellular medulla of *Peltula polyspora* (*Wetmore 17036*); A, algal layer; M, medulla; LC, lower cortex. Scale equals 50μ. -2. Thallus cross section of *Peltula euploca* (*Wetmore 14499*) showing loose medulla: A, algal layer; M, medulla; DA, dead algae; LC, lower cortex. Scale equals 50μ. 3. Section of *Peltula cylindrica* (*Wetmore 19264*) showing hollow areas in medulla; A, algal layer; H, hollow area; M, medulla. Scale equals 50μ. 4. Section of apothecium of *Heppia lutosa* (*Wetmore 13789*) showing sunken condition in thallus; H, hymenium; A, algal layer. Scale equals 100μ.

the medulla is always loose and usually has hollow areas in the center of the thallus lobes (Fig. 3).

The algae always belong to the Cyanophyceae, but in the thallus the colonies are broken up into individual cells or packets of 2–4 cells. In *Heppia* the phycobiont is *Scytonema hoffmannii* Ag. and the cells are single or in packets of two; each cell is 10–24μ in diameter. In *Peltula* the algae are *Anacystis montana* (Light.) Dr. & Daily and are in packets of 3–4 cells; the cells are 9–12μ diameter. Both of these determinations were made by Dr. Francis Drouet

from my cultures of the phycobiont. There are many extraneous algae, especially *Nostoc,* associated with the thalli and isolations must be made with care.

Algal cultures were obtained by macerating, then squashing the thallus on a slide, and finally transferring this material to a petri dish of inorganic agar. After about two to four weeks pieces of the thallus were removed from the petri dish to verify which alga was growing out of the thallus. Cultures were repeatedly transferred until uni-algal cultures were obtained.

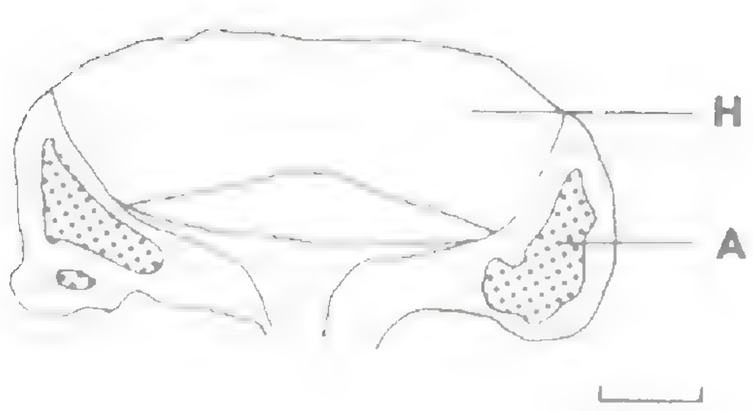
The phycobionts of *Peltula richardsii* and *P. polyspora* were studied in more detail to determine the best culture conditions. These algae were grown in uni-algal cultures under various temperatures from 16°C to 38°C (60°–100°F) and on various inorganic media. The media tried were cyanophycean agar (Starr, 1964), Henriksson's agar (Henriksson, 1964), and Bristol's agar as modified by Bold, including trace elements (Starr, 1964). Petri dishes of media were innoculated with six colonies of cells 0.4 mm in diameter and placed in growth chambers with 200 foot candles of light on 16 hour days. The cultures were allowed to grow for about 4–5 weeks at which time the colonies had grown to a maximum of 1.5 mm diameter.

The optimum culture medium for both phycobionts (both are *Anacystis montana*) was Bristol's agar and the optimum temperature was 27°C (80°F). There were minor differences in growth and appearance between the two phycobionts, but these need further study to determine their significance. The optimum temperature is somewhat higher for the algae tested than the optimum temperature of phycobionts of lichens from more moderate climates (Ahmadjian, 1967). Cyanophycean phycobionts can stand long periods of dryness, and some cultures have been made from herbarium specimens over 20 years old, although no attempt was made to determine the maximum age of collection with revivable algae.

An unsuccessful attempt was made to germinate spores of *Heppia lutosa, Peltula obscurans* var. *deserticola* and *P. richardsii.* Soaked apothecia were placed above various agar media and allowed to dry. Apothecia also were placed above agar on which the phycobiont had been growing. A few individual spores were discharged from *Heppia lutosa,* but no spores could be found from the other species, probably partly because of their small size. On two occasions spores of *H. lutosa* produced a germ tube about 20μ long at one end of the spore on Bristol's agar, but these failed to develop further. More attempts will be made when abundant fresh material of the lichens is available.

The apothecia of Heppiaceae are immersed to sessile on the upper surface of the thallus. The disc is flush with the upper surface in *Heppia lutosa, Peltula michoacanensis, P. polyspora,* and *P. richardsii* (Fig. 4). The apothecia in *P. obscurans* are first immersed then sessile or filling the whole squamule (Fig. 5). In *P. bolanderi* it is sessile with a thalloid rim. In *P. euploca, P. omphaliza, P. placodizans, P. zahlbruckneri,* and *P. cylindrica* the apothecia are totally immersed with a punctiform disc (Fig. 6). Apothecia in *P. clavata* are unknown.

The hymenium is 100–200μ thick and often pinkish in color. The epithecium of *Peltula polyspora, P. obscurans* var. *obscurans,* and *P. richardsii* always has a



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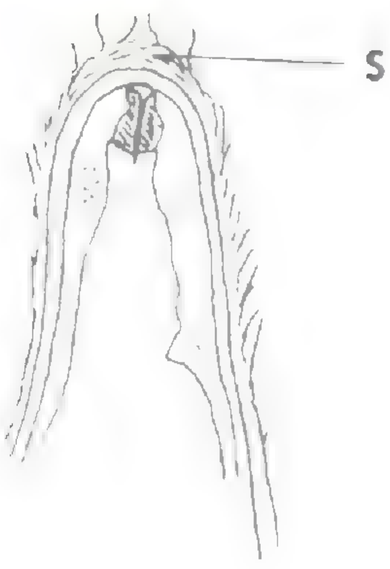

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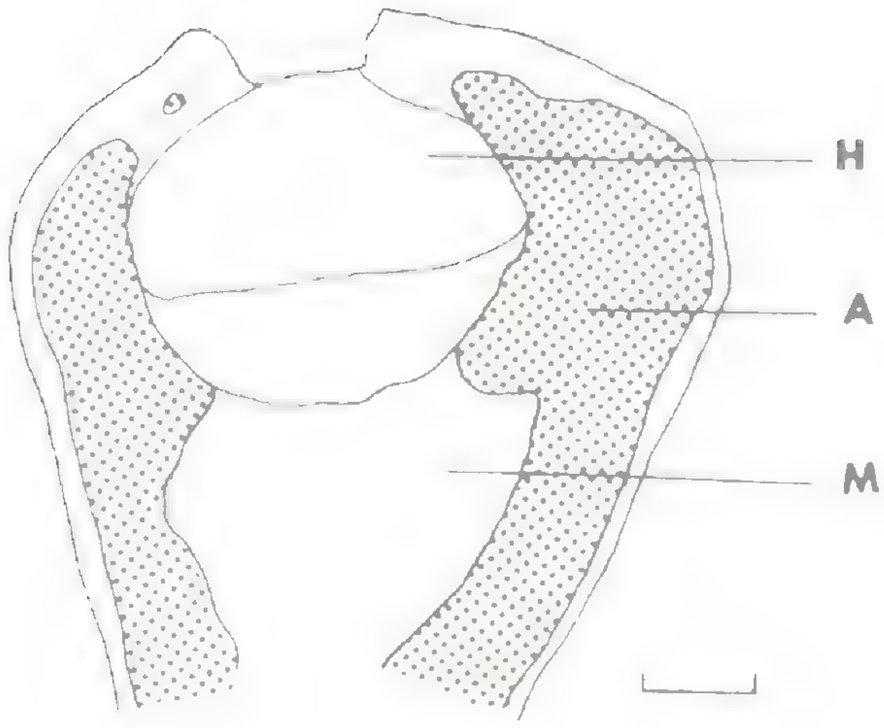

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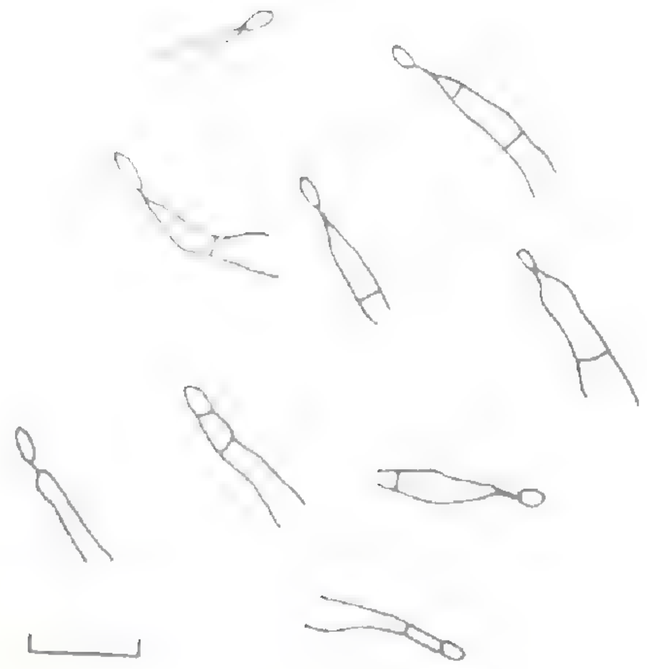

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FIGURES 5–8. Anatomy and conidiophores of North American Heppiaceae.—5. Section of apothecium of *Peltula obscurans* var. *deserticola* (*Wetmore 18294B*) showing the apothecium filling the whole squamule; H, hymenium; A, algal layer. Scale equals 100μ. —6. Section of lobe tip with apothecium of *Peltula cylindrica* (*Wetmore 19264*) showing immersed apothecium; H, hymenium; A, algal layer; M, medulla. Scale equals 100μ.—7. Ascus tip of *Peltula polyspora* (*Wetmore 14694*) showing gelatinous sheath and nature of apical apparatus; S, gelatinous sheath. Scale equals 10μ.—8. Conidiophores of *Peltula obscurans* var. *hassei* (*Wetmore 14539B*). Scale equals 10μ.

fleeting red-violet reaction as KOH or nitric acid is added to the sections on a slide under a microscope. In *P. omphaliza* and *P. placodizans* the reaction is present but is not constant. To detect this reaction it is necessary to watch the

apothecial section as the KOH is added, since the fleeting color only lasts 10–20 seconds and then fades out. Other species lack the K^+ reaction.

The paraphyses are thin (1.5–3μ) in all species except *Heppia lutosa* where they are usually thicker (3–4.6μ) and distinctly septate. The paraphyses are unbranched and capitate. The asci are usually 60–75 $\times$ 15–25μ and unitunicate. In species of *Peltula* there is a gelatinous, stringy sheath around the apex (Fig. 7), but in *Heppia lutosa* no sheath is present. The sheath is insoluble in organic solvents and strong acids and bases, but soluble in "Clorox" (a commercial preparation of calcium hypochlorite). The sheath does not stain with iodine, cotton blue, lacto-fuchsin, auto carmine, ferric chloride, or PD. There are eight spores in an ascus in *Heppia lutosa* and up to 100 or more in *Peltula*. The spores are hyaline and nonseptate in all species. Spores are oval-fusiform and large (15–24 $\times$ 6–10μ) in *Heppia lutosa*, ellipsoid and small (6–7 $\times$ 3–4μ) in *Peltula obscurans*, *P. bolanderi*, *P. michoacanensis*, *P. euploca*, and *P. omphaliza*. Spores are spherical or subspherical and small (3–7μ) in *Peltula polyspora*, *P. richardsii*, *P. placodizans*, *P. zahlbruckneri*, and *P. cylindrica*. In some older collections of *Heppia lutosa* false septa are present. These false septa are only strands of protoplasm which have also been seen by Henssen in various other genera (Henssen, 1963*a*, 1963*b*).

Pycnidia are present but not abundant on the upper surface of the thallus or in the tips of the lobes of the subfruticose thalli. Conidia are exobasidial, fusiform to bacilliform, and 3–4 $\times$ 1–2μ in size (Fig. 8).

Chemistry

The Heppiaceae in North America apparently contain none of the usual lichen substances, and none is listed by Culberson (1969). All species available (including numerous exotic species) were screened for substances extractable in hot acetone, benzene, ethyl alcohol, petroleum ether, ethyl ether, chloroform, and methyl alcohol, but no substances could be detected either by examining the residue or by the usual crystallizing reagents. No thallus reactions were detected with KOH or C in the taxa treated here. The only substance found was the pigment in the epithecium of *Peltula polyspora*, *P. richardsii*, and *P. obscurans* var. *obscurans* and occasionally in *P. omphaliza* and *P. placodizans*. This substance is not soluble in any of the above solvents, so no crystals could be detected in the crystallizing reagents. The substance is soluble in KOH and concentrated nitric acid and can be precipitated again by neutralizing the KOH or nitric acid. This substance also occurs in the thallus of some exotic species of Heppiaceae (*e.g.*, *Peltula radicata* Nyl.). It is apparently not the same as any of those in the Caloplacaceae because of its solubility properties. If any of the usual lichen substances are found in the Heppiaceae, they probably will be found in tropical material or in *Heterina*.

The value of the K^+ red-violet substance in the taxonomy of the family is variable. *Peltula polyspora*, *P. richardsii*, and *P. obscurans* var. *obscurans* constantly have the substance and therefore it is useful in identification. In *P. omphaliza* and *P. placodizans* it is not constant, although it is usually present. The main observable difference between *P. obscurans* var. *obscurans* on one hand

and var. *deserticola* and var. *hassei* on the other hand is the K+ red substance. There is no good correlation of K reaction and spore shape or lichen habitat, and so I have not recognized them as distinct species.

Distribution

Species of Heppiaceae occur mainly in the drier parts of the southwestern United States. Only six species occur outside of this area—*Heppia lutosa, Peltula euploca, P. obscurans* var. *deserticola, P. polyspora, P. cylindricia,* and *P. zahlbruckneri.*

Heppia lutosa has the widest distribution and has been collected in most parts of the United States (Fig. 29). It may be found in the remaining states and should be looked for there. *Peltula euploca* has the next widest distribution (Fig. 31) but is somewhat restricted due to substrate requirements. The greatest number of species occur in California and Arizona.

The predominant distribution type in the Heppiaceae is the Arid Southwestern according to the distribution classification proposed earlier (Wetmore, 1967). *Heppia lutosa* and *Peltula euploca* have Pan Temperate distributions, and *P. polyspora* has a Western Temperate distribution (Fig. 38).

Several species have a very restricted distribution in North America. *Peltula clavata* (Fig. 30) and *P. michoacanensis* (Fig. 32) are only known from one locality north of Mexico. *Peltula zahlbruckneri* has been found only in a few local areas near Los Angeles and Palm Springs, California, and in North Carolina (Fig. 40). Although restricted in areal distribution, *P. zahlbruckneri* is locally abundant. *Peltula cylindrica* has been collected at only five localities around Atlanta, Georgia, in the Georgia Piedmont (Jones, personal communication and Fig. 30), but too little is known of its occurrence to say much about its total distribution in North America. It may be found in other large granitic outcrops in the southern United States.

Many, if not most, of the species found in the United States will probably be found in Mexico, but few collections of Heppiaceae have been made there. Only 24 Mexican localities have come to my attention. These represent 12 taxa, all but four of which are known from areas north of Mexico. Until further collecting is done in Mexico, definitive North American distributions of Heppiaceae cannot be outlined.

Of the 15 taxa occurring north of Mexico, at least six are not known outside of North America: *Peltula bolanderi, P. obscurans* var. *deserticola, P. placodizans, P. richardsii, P. zahlbruckneri,* and *P. cylindricia.* However, *P. michoacanensis* may also occur in India, and *P. polyspora* may occur in Europe but identifications of these single collections is not certain. The most widely distributed species in the world is *Heppia lutosa.*

It can be seen that this study represents only a part of the total world distribution of most of the species. Proposed further research to cover Mexico and, eventually, the rest of the world will be necessary to determine more meaningful distribution types.

Figures 9–10. 9. Habitat of *Peltula euploca* near Boulder, Colorado. The dark track at the end of the author's hand is *P. euploca* following down a drainage crack in the rock.—10. Habitat of *Peltula cylindrica* on Mt. Arabia, Georgia, looking down-hill. The water drainage runs from bottom center to the rock crack and left. The *Peltula* borders the left side of the drainage track.

Ecology

Species of Heppiaceae are most abundant in arid and semiarid areas. All species north of Mexico grow on soil or rocks but there is one possible species of Heppiaceae in Mexico which grows on tree bark.

The species usually restricted to rock are *Peltula bolanderi, P. clavata, P. euploca, P. obscurans* var. *deserticola, P. omphaliza, P. placodizans, P. zahlbruckneri,* and *P. cylindricia.* Of these, *P. bolanderi, P. clavata, P. euploca, P. placodizans, P. zahlbruckneri,* and *P. cylindricia* are more or less restricted to noncalcareous rocks, and *P. obscurans* var. *deserticola* is usually found on calcareous rocks. *Peltula obscurans* var. *obscurans* and var. *hassei* are often on rock or soil, and *P. omphaliza* occurs on calcareous or noncalcareous rock.

Species usually restricted to soil are *Heppia lutosa, P. polyspora, P. richardsii,* and *P. michoacanensis.* The soil is usually calcareous.

In all cases a reasonable amount of substrate stability is necessary for growth. No species has been seen on loose, sandy soil, loess, clay, or soft sandstone, probably because of the rapid erosion of the surface. At one locality near Los Angeles, California, *P. euploca* was found on a large conglomerate ledge of rock, but the *Peltula* was only on the hard pebbles and not on the softer matrix. In other localities terricolous species may be found in rock cracks where soil movement is less. Some species occur only on large ledges of rock (Fig. 9). *Peltula euploca, P. bolanderi, P. zahlbruckneri,* and *P. cylindicia* were only collected on such large expanses of rock and never on small, isolated rocks (Fig. 10). *Peltula cylindrica* grows mainly in water drainage tracks on large granite outcrops (Fig. 10–11). In these tracks it often forms an almost continuous covering. Those thalli growing on higher parts of the granite show poorer growth and are not as abundant. In the eastern part of its range *Heppia lutosa* occurs only on south and southwest facing exposures on banks with sparse vegetation.

Peltula obscurans var. *deserticola* grows only on small, calcareous stones. With a little experience, suitable localities could be spotted from the road (Fig. 12). It seems to be restricted to areas with at least 30% of the soil covered with rocks between about 2 and 7 cm in diameter. When it occasionally grows on larger stones, they are not more than about 3 cm above the soil surface. In the optimum habitats with a high density of rocks, it may grow on smaller pebbles too. A possible explanation would be the need for a large enough "target area" for the lichen diaspore to land and become established. On larger stones the lichen grows near the soil surface (it is often found only as a ring near the soil surface) where moisture is greater. Sometimes the stone gets turned over, and another area of thallus will be produced until the whole stone is covered with the lichen.

Peltula bolanderi is peculiar in that it is very often found in bubble holes in lava on the underside of large boulders in lava fields (Fig. 13). In large lava beds this species may be abundant on large boulders that are almost too big to roll over. And, therefore, the lichen is very hard to collect, even if it is seen.

Peltula euploca grows in two seemingly different habitats. It is found in the mountain areas on the shaded side of rock cliffs associated with intermittent water

FIGURES 11–12.—11. Close view of a drainage track on Mt. Arabia, Georgia. The lighter areas above and below center are *Peltula cylindrica*.—12. Creosote bush desert area near Big Bend National Park, Texas, showing typical habitat of *Peltula obscurans* var. *deserticola*.

seepage (Fig. 9). *Peltula euploca* also grows on the shady side of large, very dry boulders, which probably never have water seepage.

To determine the growth rate of one species, growth rate studies were started on *Heppia lutosa* growing on a roadbank in Iowa in 1965 (Fig. 14), but frost

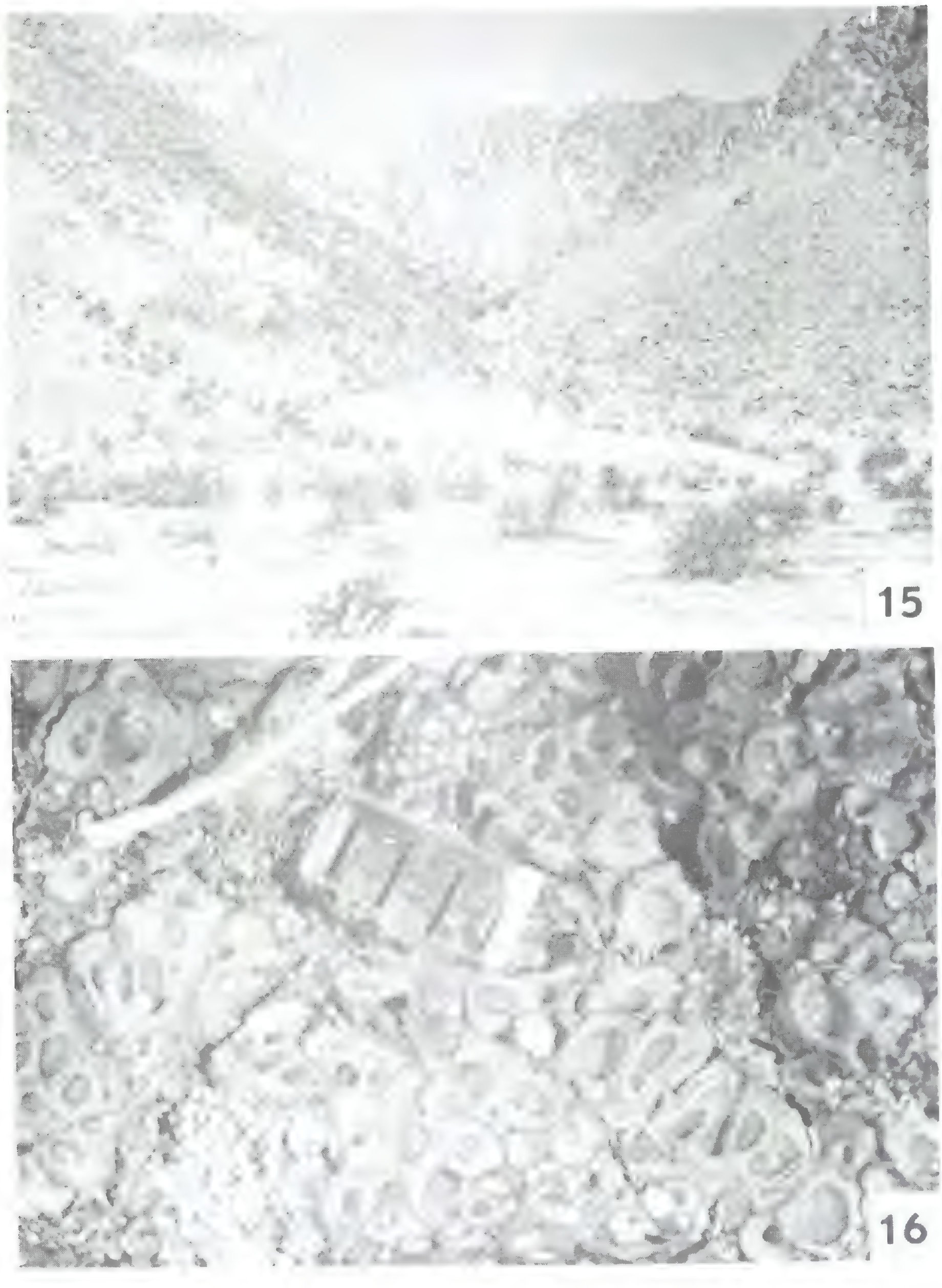
heaving and other soil movement moved the squamules so that in a one year period no evidence of growth could be seen. When this area was visited again in 1969, almost the whole colony was gone and vascular vegetation had taken over. On checking with the highway department it was found that the roadbank had been graded between 1953 and 1955. Perhaps the lack of evident growth was partly because the colony was on the decline. Some squamules placed in a pot of soil in our garden in Iowa remained the same size and normal in appearance for three years until a tremendous rainstorm covered them with soil. Pieces of thalli of *Heppia lutosa* were placed on sandy soil and loam in the greenhouse. Some were watered from below, while others were watered from above. Within a few weeks salts had accumulated over the thalli to such an extent that they were killed. However, when the pot was covered with glass to retard evaporation, no salts acculmulated, and new squamules and apothecia were produced. Pebbles with *Peltula obscurans* var. *desertícola* were placed in a covered glass dish with water in the base. These also produced new squamules after several months. The absence of Heppiaceae on soft rocks also indicates slow growth. This family is very slow to reinvade areas burned by forest fires, and it is useless to look in areas burned less than 30 to 50 years ago for Heppiaceae. In some areas of California these unburned areas are hard to find. But, on the other hand, these lichens are more abundant in drier areas where the vegetation is too sparse to support fires (Fig. 12, 15).

Except in those species with soredia, dispersal in the family is probably largely by thallus fragments. Terricolous species could easily be spread by the numerous, small whirlwinds, or dust devils, which are strong enough to pick up pieces of soil and small pebbles. Spore dispersal could be effective in the dispersal of *Heppia lutosa,* since *Syctonema* is quite common as a free living alga in arid lands. Whether only certain strains of the alga can combine with the fungus is unknown. Soredia are obviously important in the distribution as can be seen by the dense growth of *Peltula euploca* in water tracks over rock ledges (Fig. 9).

Heppiaceae are very abundant in many areas of the southwestern deserts. In many of these areas (Fig. 12, 15) most of the rocks have *Peltula obscurans* var. *desertícola,* and Heppiaceae are the dominant lichens. The growth of some terricolous species is also abundant enough to contribute significantly to soil stabilization, as seen by the extensive hyphal mat around such species as *P. richardsii* and others and the fact that terricolous thalli are usually perched on top of a mound of soil. Since many blue-green algae with heterocysts can fix atmospheric nitrogen (Fay *et al.,* 1968; Granhall & Henriksson, 1969) this family, because of its abundance, may contribute nitrates to an ecosystem which is low in available nitrates by maintaining a population of *Scytonema* in the soil. However, since no heterocysts have been recognized in the thallus, the lichen itself may not contribute to this nitrogen budget. Perhaps the felt of free-living *Scytonema* around the thallus provides nitrates for later growth of the lichen thallus.

FIGURES 13 14.—13. Habitat of *Peltula bolanderi* in central California near Death Valley. The *Peltula* grows in bubble holes on the undersides of these large lava blocks.—14. *Heppia lutosa* habitat near Greene, Iowa, on west-facing roadbank. The area just below the top of the bank had abundant *Heppia* on the bare soil.

The Heppiaceae are well adapted to desert conditions, because of the small squamules which can be easily dispersed by the wind and because of the blue-green algae which can fix nitrogen and withstand long periods of dryness. As a result, this family is slow growing, but so are the other desert plants. The species



FIGURES 15 16.—15. Habitat with Heppiaceae near Palm Desert, California. The rocks on the left side of the valley (north facing slope) had abundant *Peltula zahlbruckneri*. Other species are abundant on the smaller rocks and soil. *16. Heppia lutosa* (*Wetmore 12579*). Scale divisions are 1 mm each.

of the family are not very tolerant to competition from other plants but survive well on barren desert rocks and soil. If the squamules of the terricolous species are displaced by heavy rains, they can continue to grow in new locations, if the soil movement is not too great.

Species of Heppiaceae occur in association with several other lichens that have similar ecological tolerances. *Dermatocarpon hepaticum* (Ach.) T. Fr. usually is found in the same areas. Additional species frequently are *Lecidea decipiens* (Ehrh.) Ach. and *Sarcogyne pruinosa* (Sm. *in* Sm. & Sowerby) Körb. In some areas other associated species are *Candelariella rosulans* (Müll-Arg.) Zahlbr., *Staurothele clopima* (Wahlenb. *in* Ach.) T. Fr., *Fulgensia fulgens* (Sw.) Elenk. and species of *Acarospora, Toninia,* and other Psoras. Several species of *Acarospora* closely resemble the Heppiaceae in the field but are easily separated by the algae and spores in the lab.

Where Heppiaceae are abundant, several species may be found growing mixed together. Since most Heppiaceae grow as individual squamules, it is easy to find many combinations of *Heppia* and *Peltula* growing on the same piece of substrate.

Heppia lutosa has the broadest ecological tolerance and is found from below sea level in Death Valley, California, to above timberline at over 12,200 ft. in Colorado. Most other species occur only at lower elevations and do not reach the alpine tundra.

PHYLOGENY

I had planned to delay consideration of the phylogeny and classification of the Heppiaceae until more of the world's species had been studied but brief mention will be made now. These comments and arrangements are tentative and will certainly undergo revision as research on the family continues.

The Heppiaceae has traditionally been placed near the Pannariaceae (Zahlbruckner, 1926), but there is a strong relationship to the Collemataceae also. Both the Collemataceae and the Pannariaceae have filamentous blue-green algae, both have some species with asci with eight spores, some species with septate spores, and some species with heteromerous thalli. The Collemataceae has some species with exobasidial conidia, as does the Heppiaceae, but the Pannariaceae has endobasidial conidia. The medulla in the Collemataceae may be either cellular or loose, while the Pannariaceae has a loose medulla. The Heppiaceae probably belongs between these two families.

Within the Heppiaceae, since several of the exotic genera, such as *Neoheppia, Latzelia,* and *Pseudoheppia,* have not been studied, not too much can be said yet. There is a strong possibility that *Gloeoheppia* does not belong in this family. *Heterina* may be a distinct genus, but not enough representatives have been studied to be sure of its disposition. The final arrangement may be close to that of Gyelnik (1935). Based on North American material and a few exotic specimens, *Heppia* is probably the primitive genus followed by the more advanced and more diversified *Peltula* with the subfruticose species the most advanced, at least along the line of thallus development. If genera with septate spores are to be included in the Heppiaceae, they would be on another line of advancement. A cellular medulla is probably primitive in the Heppiaceae, while loose medulla or medulla with hollow areas would be a more advanced condition.

Taxonomy

For this study all available collections were borrowed from most of the herbaria in the United States and Canada. Many herbaria had no collections of the family. Citation of herbaria follows Lanjouw and Stafleu (1964). Specimens in several private herbaria were also studied. These are cited as HENSSEN (herbarium of Aino Henssen), KECK (Darvin Keck), SHUSHAN (Sam Shushan), SIERK (Herbert Sierk), THOMSON (John W. Thomson), and WETMORE (Clifford M. Wetmore). If no herbarium is cited for collections, they are in my personal herbarium.

On the distribution maps I have indicated by dots the locality of each collection studied except where many collections occur near each other and the dots would have completely merged. The Mexican collections seen are also mapped, but no attempt was made to borrow all Mexican collections. The collections plotted only give a rough idea of the southern extension of the ranges.

The key and descriptions are based mainly on North American material, but these should be applicable in other areas for all but the rare species. I have some other collections of Heppiaceae from the southwestern United States which I have not been able to place with any of the taxa described here. These are not described as new because they will probably be found more abundantly and better developed in Mexico or other parts of the world. However, *Peltula cylindrica* is described here because it is unlikly that this taxon occurs outside of this study area and because abundant and well developed material was available.

The listing of synonyms under each species is not complete, but includes those names directly pertinent to North America and a few other names where I have seen the types in connection with this study. Under some species numerous additional synonyms will be added as this study is expanded to include other continents.

Key to Heppiaceae of North America

1. Thallus peltate with finely sorediate margins; on rock 2
1. Thallus squamulose, peltate, or subfruticose; without sorediate margins 3
   2. Thallus small (1–2 mm diameter), thin (0.2–0.3 mm); margins deeply lobed and undulate; squamules ascending; apothecia sessile with prominent margins; dark olive-green . . . . . *Peltula bolanderi*
   2. Thallus large (3–10 mm diameter), usually thicker (0.2–0.5 mm); margins entire or deeply lobed, downrolled; apothecia usually immersed and disc punctiform; tan to olive . . . . . *Peltula euploca*
3. Thallus placodiform with distinct elongated lobes, areolate in center; with black capitate soralia on the surface; asci polysporous; spores subglobose to globose; on noncalcareous rocks . . . . . *Peltula placodizans*
3. Thallus squamulose, peltate, subfruticose, or areolate but not placodiform; not sorediate 4
   4. Apothecia expanded 5
   4. Apothecia immersed with punctiform discs or thallus without apparent apothecia 13
5. Asci with 8 spores; thallus squamulose; epithecium K−; spores 15–24 × 6–10μ; on soil . . . . . *Heppia lutosa*
5. Asci with 16–100 or more spores; spores less than 10μ long 6
   6. Epithecium K+ red-violet 7
   6. Epithecium K− 11

7. Thallus black or brown; peltate with many small apothecia or dwarf subfruticose and sterile 8
7. Thallus olive; squamulose or areolate 9
   8. Thallus peltate; many small, immersed apothecia on surface; medulla loose; spores ellipsoid, 4.6 6.1 × 3.0μ; on rock ..... *Peltula omphaliza*
   8. Thallus dwarf fruticose, finely isidiate; medulla loose with hollow areas; apothecia unknown; on noncalcareous rocks ..... *Peltula clavata*
9. Spores globose to subglobose 10
9. Spores ellipsoid to oval; medulla cellular; spores 4.5–7.6 × 3μ ..... *Peltula obscurans* var. *obscurans*
   10. Squamules large (2 6 mm diameter), concave; margin entire, downrolled; apothecia large (0.5–3 mm); medulla loose; on soil ..... *Peltula richardsii*
   10. Squamules smaller (1 4 mm diameter), flat to concave; margin entire when young, slightly lobed when older, usually thickened and upturned; medulla cellular; on soil ..... *Peltula polyspora*
11. Thallus deeply lobed, imbricate or polyphyllous, attached by umbilicus; medulla cellular; spores oval, 6.0–7.6 × 3.0–4.5μ; on soil or rock ..... *Peltula obscurans* var. *hassei*
11. Thallus only slightly lobed or entire 12
   12. Squamules deeply concave; apothecia often filling squamules, without raised thalloid rim; medulla cellular; attached by umbilicus; spores 6.1 7.7 × 3.4 4.6μ; on rock with thin layer of soil ..... *Peltula michoacanensis*
   12. Squamules convex or almost flat; apothecia with raised thalloid rim or filling squamules; medulla usually loose; attached by tuft of rhizoids or umbilicus; on rock ..... *Peltula obscurans* var. *deserticola*
13. Growing on rock 16
13. Growing on soil 14
   14. Medulla loose; squamules large (2–6 mm), concave with downturned margins; upper surface of squamules smooth; attached by tuft of few large rhizines ..... *Peltula richardsii*
   14. Medulla cellular 15
15. Broadly attached by rhizoids; often with granular margin; upper surface rough; algae in vertical columns ..... *Heppia lutosa*
15. Narrowly attached by umbilicus or few rhizines; margins often deeply lobed ..... *Peltula obscurans* var. *hassei*
   16. Thallus of scattered isolated, peltate squamules 1 3 mm in diameter; margins slightly lobed; medulla loose; several immersed apothecia per squamule ..... *Peltula omphaliza*
   16. Thallus not peltate but continuous; squamules deeply lobed or lobes inflated at tips 17
17. Thallus lobes flat, thin, deeply lobed; medulla cellular ..... *Peltula obscurans* var. *hassei*
17. Thallus lobes swollen and inflated; medulla loose with hollow areas 18
   18. Thallus close to substrate, not over 1 mm tall; apothecia usually present but immersed ..... *Peltula zahlbruckneri*
   18. Thallus subfruticose, often to 4–7 mm long, ascending, branched 19
19. Lobes terete, not offset, usually one immersed apothecium in the tip of a lobe ..... *Peltula cylindrica*
19. Lobes flattened and offset, fertile lobes often larger and with several immersed apothecia per lobe ..... *Peltula tortuosa*

HEPPIACEAE

Heppiaceae Zahlbr. *in* Engler & Prantl, Nat. Pfl. 1(1*): 176. 1906. Tribe Heppieae Müll.-Arg., Mém. Soc. Phys. Hist. Nat. Genève 16: 377. 1862.

Thallus squamulose to areolate or peltate or subfruticose, heteromerous, paraplectenchymatous throughout or with loose hyphae in the medulla or with hollow areas; apothecia totally immersed or sessile; discs punctiform or open; asci clavate, containing 8–100 or more spores; paraphyses simple and unbranched;

spores hyaline, nonseptate or septate; conidia exobasidial; phycobiont members of Cyanophyceae.

Heppia Naeg. *in* Hepp

Flecht. Eur. 49. 1853. TYPE: *Heppia urceolata* (Schaer.) Naeg. *in* Hepp [= *Heppia lutosa* (Ach.) Nyl.].

Thallus squamulose, broadly attached by hyphae, more or less paraplectenchymatous throughout, usually with a distinct medulla; asci with 8 spores, without gelatinuous sheath, spores hyaline, non-septate; phycobiont *Scytonema*.

Heppia lutosa (Ach.) Nyl., Syn. Lich. 2: 45. 1855.

Collema lutosum Ach., Syn. Lich. 309. 1814. *Pannaria lutosa* (Ach.) Nyl., Actes Soc. Linn. Bordeaux 21: 314. 1856 (= Prod. Lich. Gall. Alger.). *Heppia urceolata* var. *lutosa* (Ach.) Boist., Nouv. Fl. Lich. 2: 87. 1903. TYPE: Germany, "ad terram limosam." (H, not seen.)

Solorina despreauxii Mont. *in* Webb & Berth., Hist. Nat. Isles Canar. 3(2): 104. *pl. 6, f. 5.* 1840. *Heppia despreauxii* (Mont. *in* Webb & Berth.) Tuck., Gen. Lich. 46. 1872. *Solorinaria despreauxii* (Mont. *in* Webb & Berth.) Fink, Lich. Fl. United States 170. 1935. *Solorina virescens* Mont. *in* Webb & Berth., Hist. Nat. Isles Canar. 3(2): 104. 1840. *Heppia virescens* (Mont. *in* Webb & Berth.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 110. 1857. *Heppia lutosa* * *H. virescens* (Mont. *in* Webb & Berth.) Nyl., Syn. Lich. 2: 45. *pl. 9, f. 31.* 1885. TYPE: "Ad terram humidam in montibus insulae Canariae," *Despréaux*. (Possible isotype H-NYL.)

Endocarpon urceolatum Schaer., Enum. Crit. Lich. Eur. 233. 1850. *Heppia urceolata* (Schaer.) Naeg. *in* Hepp, *Flecht. Eur. 49.* 1853. TYPE: "Ad terram in m. Gemmi, *Schaer.* in Lozère *Prost.*" (Not seen.)

Lecanora adglutinata Kremp., Flora 34: 675. 1851. *Heppia adglutinata* (Kremp.) Mass., Geneac. Lich. 8. 1854. *Pannaria adglutinata* (Kremp.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 2: 324. 1854. *Heppiomyces adglutinatae* (Kremp.) Cif. & Tom., Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia Atti. Ser. 5.10: 77. 1953. TYPE: "südbaverischen Alpen." (Not seen.)

Heppia conchiloba Zahlbr., Beih. Bot. Centralbl. 13: 157. 1902. TYPE: California. Palm Springs, in lateribus orientalibus montim San Jacinto, *Hasse FN 823*, 1901. (Holotype W.)

Heppia macrospora B. de Lesd., Ann. Cryptog. Exot. 5(2): 113. 1932. TYPE: New Mexico. Las Vegas, Kearny's Gap, *Arsène 20091*, 1927. (Lectotype US; isotype FH.

NOMENCLATURAL REMARKS. Degelius (1954) studied the type of *Collema lutosum* Ach. and referred it to *Heppia* where it takes priority over the other names which were in use. I have seen photographs of the type material in the Acharian herbarium in Helsinki but was unable to come to any conclusions based on them, and I will accept the findings of Degelius. There is a specimen on the same sheet from France, but since Acharius only mentions material from Germany, that must be considered the holotype.

Solorina virescens Mont. *in* Webb & Berth. was used as a synonym under *Solorina despreauxii* in the original description, and so is an obligate synonym based on the same type. Two collections were seen from the Canary Islands (H-NYL 30920 and 30921). These are probably duplicates of the type material.

The holotype of *Heppia macrospora* B. de Lesd. was probably destroyed, and I am selecting the isotype in US as the lectotype.

Thallus squamulose (Fig. 16), tan to dark olive; squamules 1–7 mm diameter, concave or flat, roundish to irregular or elongated and folded but not

deeply lobed; margins of larger squamules sometimes granular; upper surface rough and cracked; attached over most of the lower surface by large septate hyphae 7.6–12.1μ thick. Thallus 214–275μ thick; upper cortex 30μ thick; lower cortex inseparable from cellular medulla; algal layer 150–210μ thick, often filling most of the thallus; algal cells in columns, clumped in pairs of cells or as single cells. *Apothecia* usualy one per squamule (rarely up to 10), immersed in upper surface of thallus (Fig. 4); discs expanded, 0.5–1.5 mm, without thalloid rim; epithecium yellowish brown, K ; hymenium 103–120μ thick; paraphyses 3.0–4.6μ thick, obviously septate with large lumina; asci without gelatinuous sheath, 68 × 23μ, containing 8 spores; spores hyaline, nonseptate, fusiform, 15–24 × 6.8–10.3μ. *Hymenium* I^+ wine-red. *Conidia* fusiform 4.9–6.1 × 1.8–2.4μ.

This species has a Pan-Temperate distribution in North America (Fig. 29). It grows on calcareous soil throughout the United States and north to the Canadian prairie with one collection from the Arctic Slope of Alaska. Common on bare soil and soil banks (Fig. 13).

TAXONOMIC REMARKS. A form with large squamules and granular margins was described by Zahlbruckner as *H. conchiloba,* but the granules are not normal soredia. They are produced by a cracking of the margin and are of no taxonomic significance but may serve the same function as soredia in dispersal.

Exsiccati: *Plitt, Lich. Exs. 34* (sub *Heppia despreauxii*) (DS, FH, MU), 239 (sub *Heppia terrena*) (ABS, MU).

STATE UNKNOWN. Mexican Boundary Survey, mainly in the valley of Rio Grande, *Wright* (FH). Colorado City, *Schantz*, 1904 (MICH).

ALABAMA. COUNTY UNKNOWN: *Peters*, 1874 (FH, MO, US).

ALASKA. At Franklin Bluffs on the Sagavanirktok River, *Thomson, Shushan & Koranda 6493* (WIS).

ARIZONA. COCHISE CO.: Chiricahua Mts., Cave Creek 6 miles W of Portal, *Weber & Shushan S-8797* (COLO); trail to Silver Peak and Headquarters Gulch, *Weber, Shushan & Anderson*, 1960 (COLO, DUKE, PAC, UC). COCONINO CO.: Grand Canyon National Park, South Rim, along Hermit's Rest Trail, *Wetmore 14978*; South Rim, Rowes Well Road near edge of Park, *Wetmore 15019*. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14534B*. Sauceda Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14543C*. MOHAVE CO.: In Detrital Valley SW of Hoover Dam on US 93, *Wetmore 14896*. 27 miles E of Kingman near Hackberry along US 66, *Wetmore 14904*. PIMA CO.: Tucson, Station I, *Blumer*, 1908 (MICH). Saguaro National Monument NW of Tucson, *Wetmore 14516B*. YUMA CO.: Near Mohawk, E of Yuma on US 80, *Wetmore 14544B, 14547A, 14548A*.

CALIFORNIA. IMPERIAL CO.: Near Salton City on west side of Salton Lake, *Wetmore 14551*. INYO CO.: Death Valley National Monument near junction of California 190 and Nevada 58, *Wetmore 14877A*. KERN CO.: E of Maricopa on California 166, *Wetmore 14800A, 14805*. LOS ANGELES CO.: Santa Monica Range, *Hasse* [13 specimens collected between 1897 and 1905] (ABS, DS, FH, LAM, MINN, MU, NY, POM). Newhall, *Farlow*, 1897 (FH). Near Soldier's Home, *Hasse*, 1897 (UC). San Clemente Island, between Eel Point and Seal Cove, *Weber & Santesson L-43631* (COLO). RIVERSIDE CO.: S of Cathedral City, *Wetmore 16863*. Near western edge of Palm Desert, *Wetmore 16847*. Palm Springs, *Hasse FN 823 p.p.* (W). San Jacinto Mts., west edge of Palm Springs in Chino Canyon, *Wetmore 14625A*. In Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16877*. Near Riverside, Joshua Tree National Monument, *Sipe 1367* (COLO). SAN BERNARDINO CO.: Near Barstow, *Jaeger*, 1932 (F). SAN DIEGO CO.: San Diego, *Cleveland*, 1875 (US).

COLORADO. BACA CO.: SW of Utleyville, vicinity of Dodge Ranch, *Shushan S-8156* (COLO). BOULDER CO.: Steamboat Mt., southwest base, 2 miles NW of Lyons, *Weber*,

Anderson & Awasthi S-17946A (COLO); southwest slope 1.5 miles NW of Lyons, *Wetmore 16138, 16165, 16183;* south base 1.5 miles N of Lyons, *Weber & Shushan* S-17946 (COLO, SHUSHAN); west slope 2 miles NW of Lyons, *Weber 1 9901* (COLO). Rocky Mt. National Park, Wild Basin, *Anderson 2122* (COLO). CHAFFEE-GUNNISON COS.: Lake Pass, Sawatch Mts., *Imshaug 11781* (MSC). CONEJOS CO.: 1 mile E of Manassa, *Wetmore 17264*. CUSTER CO.: South Colony Creek, *Kiener 10270* (F). ELBERT CO.: 10 miles NW of Lemon, *Shushan Sl-299* (SHUSHAN). GRAND CO.: Rocky Mt. National Park, 1 mile E of Grand Lake, base of S slope of Mt. Enentah, *Anderson 3467* (COLO, WETMORE); NE of Grand Lake between Summerland Park and Cascade Falls of North Inlet, *Anderson 3254* (COLO). LARIMER CO.: Rocky Mt. National Park, at mouth of Fall River Canyon SE of Endovalley Campground, *Wetmore 15909*; Mummy Range, SE of Lawn Lake, base of Mummy Mt., *Anderson 2064* (COLO); Mummy Range, Mt. Chiquita, *Anderson 2905* (COLO). 22 miles N of Ft. Collins, 2 miles SE of Table Mt., *Anderson S-20233* (ABS, COLO). 19 miles N of La Porte, *Shushan & Weber S-2346* (COLO). Owl Canyon, 9.7 miles N of "Teds Place" (junction of highways 28 and 14), *Shushan & Weber S-4793* (CANL, COLO, FH). 0.5 miles S of Wyoming state line (just N of Virginia Dale), *Shushan Sl-1517* (SHUSHAN). LAS ANIMAS CO.: W of Carrizo Creek, S. of Utleyville, *Shushan S-8121* (COLO). LOGAN CO.: 6 miles S of Peetz, *Shushan Sl-319* (SHUSHAN). MESA CO.: N of Colorado National Monument, 3 miles S of Fruita, *Shushan & Weber S-4993* (ABS, CANL, COLO, FH). MONTEZUMA CO.: 22 miles SW of Towaoc, *Shushan & Weber S-680* (COLO). PETKIN CO.: Elk Mts., trail from Conundrum Pass to Conundrum Hot Springs Guard Station, *Weber & Shushan S 5980* (COLO). SUMMIT CO.: Loveland Pass, *Wetmore 16332*. WELD CO.: Eastern end of Chalk Bluffs, 3 miles S of Wyoming state line (Cox Ranch), *Shushan S-2533* (COLO, DUKE, LAM, WIS). 0.5 mile SW of Twin Pawnee Buttes, *Shushan & Higgins S-4900* (COLO, US, WTU). YUMA CO.: 6 miles E of Wray, *Shushan & Anderson L-32966* (COLO). Wray, high plains, *Kiener 6362* (F, WTU). South edge of Wray, *Wetmore 15742*.

FLORIDA. COUNTY UNKNOWN: *Calkins s.n.* (MICH). OSCEOLA CO.: Ashton, *Moore 6244* (WETMORE). POLK CO.: 7 miles E of Avon Park, *Wetmore 13789*. SEMINOLE CO.: Markham, *Rapp*, 1929 (YU). Sanford, *Rapp*, 1912 (FH, US). VOLUSIA CO.: Daytona, *Thaxter 243* (FH, MICH).

GEORGIA. MCINTOSH CO.: Darien, *Ravenel*, 1882 (PH).

ILLINOIS. COUNTY UNKNOWN: *Calkins s.n.* (F), *Hall*, 1879 (FH, US). FULTON CO.: Canton, *Miller 72* (BKL), *Wolf* (PH, US). MENARD CO.: Athens, *Hall*, 1862 (F, FH, WIS). MONROE CO.: Fults, *Skorepa 1853* (WETMORE).

IOWA. BUTLER CO.: 3 miles S of Greene along Iowa 14, *Wetmore 12579*. CLAYTON CO.: Pikes Peak, bluffs along Mississippi River near McGregor, *Imshaug 27883* (MSC). FAYETTE CO.: *Fink*, 1894 (ABS, CANL, CINC, CUP, F, FH, MICH, MINN, MO, MU, NY, OS, POM, US, WIS, THOMSON). 2.5 miles W of Fayette on highway 93, *Niemann 33* (WETMORE). WINNESHIEK CO.: E of Decorah, *Wetmore 15451*.

KANSAS. FRANKLIN CO.: 1 mile SW of Ottawa, *Kramer 483* (WIS). LEAVENWORTH CO.: 4 miles NE of Tonganoxie, *McGregor 1428* (MO). LOGAN CO.: 4 miles SW of Eldadeer, *McGregor 2151* (MO).

MASSACHUSETTS. MIDDLESEX CO.: Cambridge, opposite Mt. Auburn gate, *Tuckerman*, 1853 (FH).

MINNESOTA. BROWN CO.: New Ulm, *Fink 284* (MINN). BLUE EARTH CO.: Mankato, *Fink 177* (MINN). KANDIYOHI CO.: Locality unknown, *Looman*, 1961 (WIS). OTTER TAIL CO.: Battle Lake, *Fink 57* (MINN). Leaf Hills, *Fink 232* (MICH, MINN, US). PENNINGTON CO.: Thief River Falls, *Fink 773* (MINN). YELLOW MEDICINE CO.: Granite Falls, *Fink 507* (MINN).

MISSOURI. FRANKLIN CO.: Missouri Botanical Garden Aboretum, Gray Summit, *Anderson*, 1949 (CUP). JEFFERSON CO.: Crystal City, *Russell 142* (MICH, MO). PERRY CO.: Perryville, *Demetrio 13* (NY, PH).

MONTANA. CUSTER CO.: 10 miles SW of Miles City along US 10, *Wetmore 12840, 12846*. DAWSON CO.: 10 miles SW of Glendive, *Wetmore 12783, 12786, 12790B, 12793, 12807*. ROOSEVELT CO.: Locality unknown, *Looman*, 1961 (CANL, WIS). ROSEBUD CO.: W of Forsyth above campground, *Wetmore 12870*.

NEBRASKA. CASS CO.: 4 miles SE of Elmwood, *Kiener 13637* (COLO). CHERRY CO.: In city park in Valentine, *Wetmore 13094A*. CUSTER CO.: 2 miles E of US 183 on Nebraska 92 (21 miles W of Loup City), *Wetmore 13112, 13113*. DODGE CO.: Fremont, *Kiener 24413*

(WETMORE). HARLAN CO.: Along US 6, 8 miles S of Atlantic, *Wetmore 15714*. LANCASTER CO.: 7 miles NW of Lincoln, *Kiener 9704* (F, FH, WTU). POLK CO.: 4 miles E of Platte River along Nebraska 92, *Wetmore 13118*. SARPY CO.: S of Melia, *Kiener 8274* (F).

NEVADA. CLARK CO.: Along US 91 NE of Las Vegas 22 miles at road to Axial, *Wetmore 17035B, 17039*. Near Gold Butte, *Tavares 31d* (UC). NYE CO.: Near Mercury along US 95, *Wetmore 14894A*.

NEW MEXICO. LINCOLN CO.: Carrizozo, Tularosa Basin Las Vegas, *Shields 21, Shields 7, Shields 6a* (all WTU). MCKINLEY CO.: Cibola National Forest at Quaking Aspen Campground, SE of Gallup, *Wetmore 15132, 15134*. Along US 66 at road to Manvelito 13 miles W of Gallup, *Wetmore 15076*. OTERO CO.: Lincoln National Forest, 2 miles E of Mountain Lake (F of Alamagordo), *Wetmore 14412*. SAN JUAN CO.: 7 miles F of Blanco, *Shushan S-7906* (ABS, COLO, MSC). SAN MIGUEL CO.: Las Vegas, Kearny's Gap, *Arsène 20091* (FH, US), Agua Zarca, *Arsène 19698* (FH, US). Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15159, 15161*. 3 miles F of Las Vegas on New Mexico 65, *Wetmore 15144*. TAOS CO.: 4 miles S of Tres Piedras, *Shushan & Weber S-6547* (COLO). UNION CO.: Capulin Mt. National Monument, *Wetmore 15200*. 3 miles N of Capulin Mt. National Monument, *Wetmore 17421, 17468, 17472*. 7 miles E of Folsom, *Shushan S-11407* (COLO). VALENCIA CO.: Along San Jose River, 3.5 miles SE of Correo on road to Las Lunas, *Shushan & Weber S-6890* (COLO).

NEW YORK. ROCKLAND CO.: Tomkins Cove, *Fleming, Fleming & Nearing*, 1963 (COLO, NY, NYS). WARREN CO.: Glen's Falls, *Willey*, 1872 (US).

NORTH CAROLINA. COUNTY UNKNOWN: *Curtis* (FH).

NORTH DAKOTA. BILLINGS CO.: S of Medora in North Dakota Badlands, *Wetmore 12768*. NORTON CO.: 4 miles W of Mandon along US 10, *Wetmore 12769*.

OHIO. HAMILTON CO.: Cincinnati, *Lea*, 1843 (FH, PH, US).

OKLAHOMA. MARSHALL CO.: Near Happy Hollow, *Keck 1773* (KLCK). MURRAY CO.: Platt National Park, *Wetmore 14120*. TEXAS CO.: 7 miles NE of Guyman on US 54, *Wetmore 15227*.

SOUTH CAROLINA. COUNTY UNKNOWN: Locality unknown, *Tuckerman* (BUK), *Curtis* (NYS). AIKEN CO.: Santee District, Aiken, *Ravenel 465* (FH). DARLINGTON CO.: Society Hills, *Curtis*, 1850 (FH, NY).

SOUTH DAKOTA. CUSTER CO.: 3.6 miles S of US 16 on Fourmile Creek Road (4 miles W of Custer), *Wetmore 6705* (MSC). LAWRENCE CO.: Spearfish Canyon S of Bridal Veil Falls (6 miles S of Spearfish), *Wetmore 11107* (MSC). 5 miles NW of Spearfish, *Wetmore 11191* (MSC). PENNINGTON CO.: 3 miles WSW of Rapid City, E of Dark Canyon, *Anderson S-20580* (COLO, MSC). Matt Burn, 2 miles SE of Deerfield Reservoir, *Wetmore 12524*. E of Hayward (15 miles SSW of Rapid City), *Wetmore 11058* (MSC, WETMORE), *Wetmore 11038, Wetmore 11044* (both MSC).

TENNESSEE. ANDERSON CO.: Savage's Garden, *Sharp*, 1957 (WIS). HAMILTON CO.: Chattanooga, *Calkins*, 1892 (PH). Mission Ridge, *Calkins s.n.* (CUP, F, FH, MICH, MINN, MO, NY, PAC, THOMSON).

TEXAS. COUNTY UNKNOWN: Locality unknown, *Wright*, 1852 (FH); Mexican Boundary Survey, in valley of Rio Grande below Doñana, Hills of the Blanco, *Wright*, 1850 (FH); Organ Mts., *Wright 58, 32* (FH). BREWSTER CO.: Big Bend National Park, along Lost Mine Trail from Panther Pass, *Wetmore 14265B*; 2 miles W of junction with road to Castolon, *Wetmore 18303*; Dagger Flats, *Wetmore 18205, 18215*; Hot Springs near Rio Grande Village, *Wetmore 18189, 18193*; Old Mine Road near Rio Grande Village, *Wetmore 18377, 18381*; Pulliam Ridge, *Wetmore 18203A*. BROWN CO.: SW of Brownwood on US 67, *Wetmore 14209, 14211*. CAMERON CO.: NE of Resaca Park, Brownsville, *Runyon 3819a* (MO). JOHNSON CO.: Cleburne State Park (SW of Cleburne), *Wetmore 14163, 14190*. REEVES CO.: N of Pecos along US 285, *Wetmore 14313, 14317B*. UPTON CO.: N of McCamey in King Mt. area, *Wetmore 14243*.

UTAH. EMERY CO.: San Rafael River, Buckhorn Wash, *Flowers 892* (COLO). GRAND CO.: Delores River, 1 mile E of junction with Colorado River, *Flowers 1057* (COLO). KANE CO.: Colorado River at Rock Creek, *Flowers 807* (COLO, DUKE). UINTAH CO.: Dinosaur National Monument, mouth of Split Mountain Gorge, *Anderson, Awasthi & Dahl S-29387* (COLO, DUKE). WASHINGTON CO.: 13 miles W of Santa Clara along US 91, W of St. George in Shivwits Indian Reservation, *Wetmore 17056*.

VERMONT. RUTLAND CO.: Wallingford, *Schallert 18168* (F).

WISCONSIN. DANE CO.: Madison, collector unknown (WIS). IOWA CO.: Mill Creek, 6 miles W of Arena, *Wetmore 13175, 13217.*

WYOMING. CARBON CO.: Snowy Pass, Medicine Bow National Forest, 43 miles E of Laramie, *Shushan S-9830* (COLO).

SASKATCHEWAN. ASSINIBOIA CO.: Locality unknown, *Looman,* 1961 (WIS, CANL).

Specimens also seen from Mexico, Bermuda, Canary Islands, and Europe.

Peltula Nyl.

Ann. Sci. Nat. Bot. Sér. 3. 20: 316. 1853 and Mém. Soc. Sci. Nat. Cherbourg 2: 322. 1853. *Heppia* sect. *Peltula* (Nyl.) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215, footnote. 1890). TYPE: *Peltula radicata* Nyl.

Endocarpiscum Nyl., Flora 47: 487, footnote. 1864. TYPE: *Endocarpiscum guepinii* (Del. *in* Duby) Nyl. [= *Peltula euploca* (Ach.) Wetm.].

Guepinia Hepp, Verh. Schweiz. Naturf. Ges. 48: 85. 1864. TYPE: *Guepinia polyspora* Hepp [= *Peltula euploca* (Ach.) Wetm.].

Guepinella Bagl., Nuovo Giorn. Bot. Ital. 2: 174. 1870. TYPE: *Guepinella myriocarpa* Bagl. [= *Peltula euploca* (Ach.) Wetm.].

Heppia sect. *Pannariella* Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215. 1890). *Pannariella* (Wain.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. TYPE: *Pannariella bolanderi* (Tuck.) Gyel. [= *Peltula bolanderi* (Tuck.) Wetm.].

Heppia sect. *Placoheppia* Zahlbr., Bull. Torrey Bot. Cl. 35: 300. 1908. *Solorinaria* sect. *Placoheppia* (Zahlbr.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. *Placoheppia* (Zahlbr.) Oksn., Fl. Lich. Ucrain. 1: 407. 1956 (*comb. inval.*). TYPE: *Heppia placodizans* Zahlbr.

Thallus areolate, squamulose, peltate or subfruticose, attached by small area of rhizines or umbilicus; paraplectenchymatous throughout or with loose medulla; asci with 16–100 or more spores, with gelatinous sheath; spores hyaline, non-septate; phycobiont *Anacystis.*

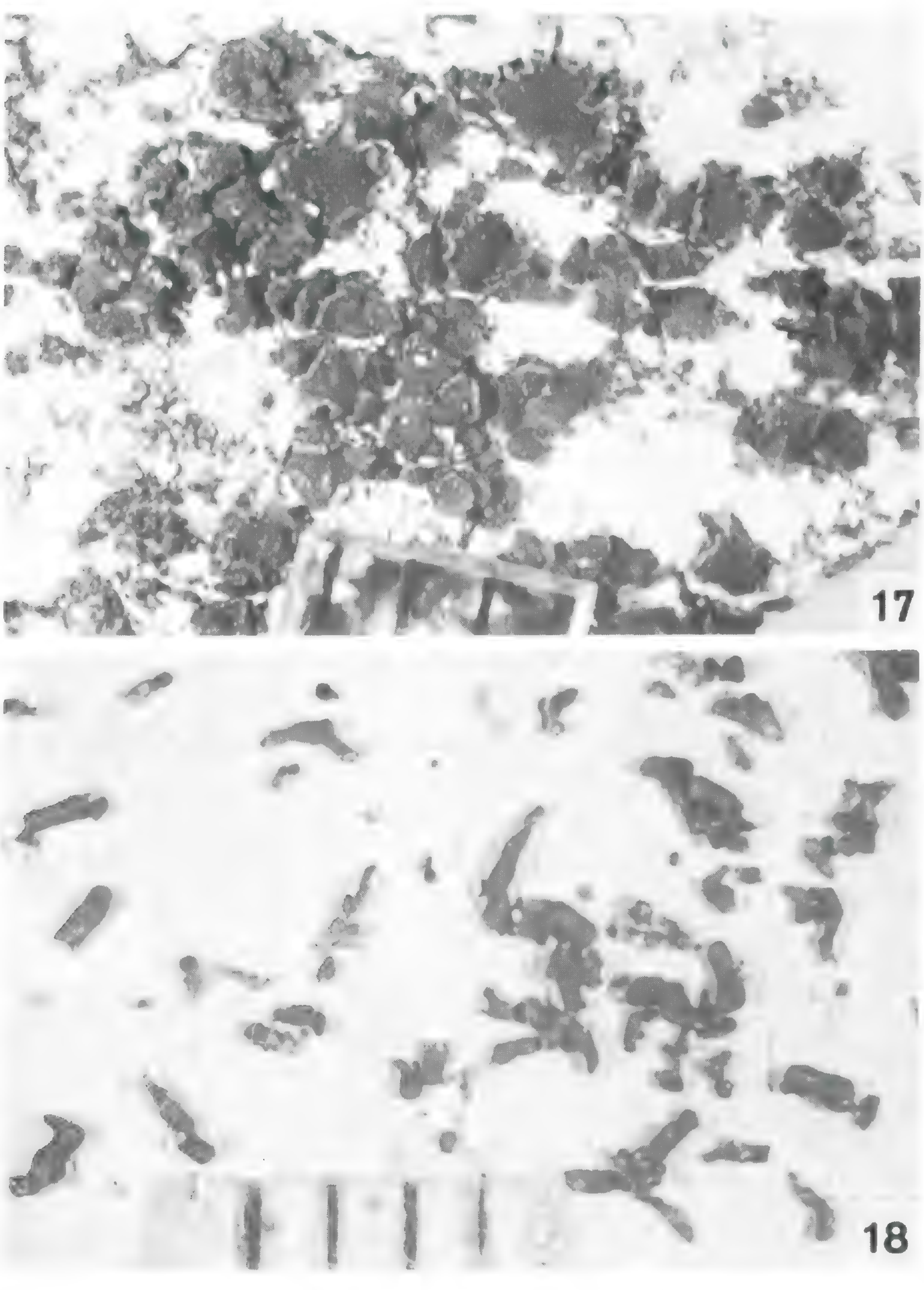
NOMENCLATURAL REMARKS. The type of *P. radicata* in H-NYL has been examined, and although the algae have not been cultured, the other characters of the recircumscription agree well with *P. radicata.*

Endocarpiscum, Guepinia, and *Guepinella* were described to separate the polysporous species from the octosporous species, however, *Peltula* was described first. *Heppia* sect. *Placoheppia* was described as a new section for *Heppia placodizans,* however, I do not feel that the differences are significant enough to warrant this separation.

Peltula bolanderi (Ach.) Wetm., comb. nov.

Pannaria bolanderi Tuck., Gen. Lich. 51, footnote. 1872. *Endocarpiscum bolanderi* (Tuck.) Tuck., Syn. N. Amer. Lich. 1: 114. 1882. *Heppia bolanderi* (Tuck.) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215. 1890. *Pannariella bolanderi* (Tuck.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. TYPE: California. Ukiah, on rocks, *Bolander 242.* (Holotype FH-TUCKERMAN, isotype FH.)

Thallus peltate (Fig. 17), dark olive-brown; squamules small (1–2 mm diameter), lobed and somewhat polyphyllous; margins ascending, undulate, sorediate; attached by umbilicus. Thallus lobes 214–336μ thick; no upper cortex; lower cortex of several layers of cells, 60–75μ thick; medulla of loose hyphae; algal layer 105-150μ thick. *Apothecia* rare, 3–8 per squamule, at first totally immersed then sessile with small thalloid rim; discs 0.3–0.5 mm diameter;



FIGURES 17–18.—17. *Peltula bolanderi* (*Wetmore 16789*). Scale divisions are 1 mm each.—18. *Peltula cylindrica,* lobes broken from thallus (*Wetmore 19264*). Scale divisions are 1 mm each.

epithecium light yellow, K—; hymenium 150–170μ thick; paraphyses capitate, 1.5–3μ thick; asci with gelatinous sheath, containing 100 or more spores; spores ellipsoid to fusiform, 6.0–7.6 $\times$ 3.0–4.5μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 3.1–3.7 $\times$ 1.2μ.

This species has an Arid Southwestern distribution in North America (Fig. 30) and grows on rock that is usually noncalcareous but also rarely on calcareous rocks or on plant detritus. It occurs in shaded or more moist localities than some *P. euploca.* It frequently occurs in bubble holes on the undersides of large chunks of lava (Fig. 12).

Taxonomic Remarks. This species is similar to *P. euploca,* but *P. bolanderi* has upturned lobe margins, is darker in color, smaller, thinner, and has more undulate margins. The apothecia have a small thalloid rim. Some collections from California contain thalli of both species growing side by side and have no intermediates.

Exsiccati: *Plitt, Lich. Exs. 138* (ABS, FH, MU), *139* (sub *Heppia polyspora*) (ABS, FH). *Zahlbruckner, Lich. Rar. 90* (FH).

Arizona. maricopa co.: Sauceda Mts., 14 miles S of Gila Bend, *Wetmore 14543D.* mohave co.: W of Burro Creek Crossing, *Darrow,* 1947 (LAM).

California. county unknown: *Bolander* (MICH), *Hasse* (F), Laguna Creek, Santa Cruz Peninsula, *Herre 1233* (DS, FH, NY). alameda co.: Oakland Hills, *Bolander 98 p.p.* (FH). inyo co.: 10 miles N of Independence on US 395, *Wetmore 16757.* los angeles co.: *Hasse* (FH, THOMSON). Santa Monica Range, *Hasse,* 1896 (DS); *Hasse,* 1903 (NY); *Hasse,* 1905 (ABS, FH); *Hasse,* 1907 (US); *Hasse,* 1911 (US); *Hasse,* 1912 (ABS); *Hasse,* March, 1915 (FH), *Hasse,* May, 1915 (ABS, FH, MU); Topanga Canyon, *Hasse,* 1907 (NY), 2 miles N of Coldbrook Station along California 39 near Azuza, *Wetmore 16781, 16789, 16802, 16805.* Near San Fernando, *Hasse,* 1908 (FH). Foothills Santa Monica Range near Soldiers Home, *Hasse,* 1911 (LAM). mendocino co.: Ukiah, *Bolander 242* (FH). monterey co.: Carmel Valley, Hastings Natural History Reservation, *Tavares 792a* (UC). riverside co.: Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16881C.* San Jacinto Mts., south edge of Banning, *Wetmore 14629 p.p.* (sub *P. euploca*); above Soboba Hot Springs, NE of Hemet, *Wetmore 14702B.* santa clara co.: Alum Rock Park, *Baltzo,* 1968 (WETMORE), *Tavares & Baltzo 2268* (WETMORE). santa cruz co.: Santa Cruz, *Hasse* (MICH).

New Mexico. san miguel co.: Keary's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15152.* union co.: Capulin Mt. National Monument, *Wetmore 15188.* 3 miles N of Capulin Mt. National Monument, *Wetmore 17436.*

Utah. washington co.: E of Santa Clara along US 91, *Wetmore 17078.*

Peltula clavata (Kremp.) Wetm., comb. nov.

Heterina clavata Kremp., Flora 49: 56. 1876. *Heppia clavata* (Kremp.) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 214. 1890 (= Étude Lich. Brésil. 1: 214. 1890). type: Brasil. "Collecti a D. A. Glaziou in provincia brasiliensi Rio Janeiro," ad rupes. (Not seen).

Thallus minutely subfruticose, black to greenish-black; lobes 0.5–1 mm long, 0.5–1 mm wide at tips, branched or slightly lobed or sometimes flattened at tips, surface with scattered minute isidia; attached by umbilicus. No cortices present; medulla of loose hyphae with hollow areas; algal layer 25–50μ thick. *Apothecia* unknown. *Conidia* fusiform, 3.7–4.3 $\times$ 1.2-1.8μ.

Only one collection is known from north of Mexico. It was growing on noncalcareous rock probably in a moist habitat (Fig. 30).

Taxonomic Remarks. I have only seen a few collections of this species, and therefore the circumscription is provisional. It belongs in *Peltula,* but apothecia must be found to confirm this. The blackish, insidiate thallus helps to distinguish it from other species of *Peltula.*

ARIZONA. COCHISE CO.: Chiricahua Mts., on trail to Silver Peak and Headquarters Gulch, NE of Southwestern Research Station, *Weber, Shushan & Anderson S-24627* (COLO).

Specimens also seen from Mexico and Brasil.

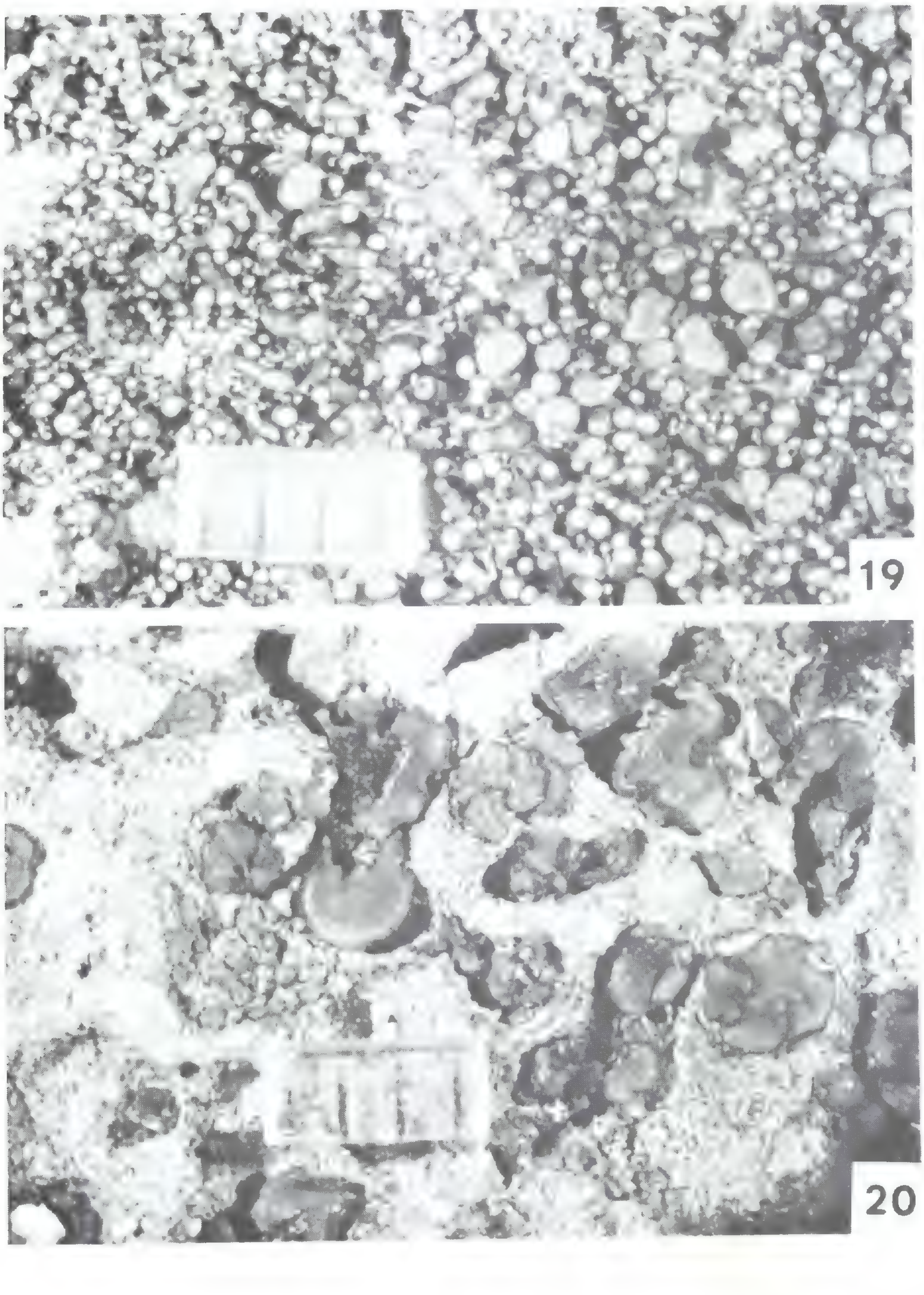
Peltula cylindrica Wetm., sp. nov.

Thallus subfruticulosus, fusco-olivaceus cum crescentibus aspicibus levius pigmentum, formans areas continuas super subtratum; lobi cylindrici, recti, aliquanti ramosi, aspices interdum aliquanti complanati, stipes interdum leviter prolificus vel complanatus, juvenillus squamae leviter peltatae, facies laevigata; soredia et insidia desunt; squama affixa per umbilicum. Thalli lobi 296–741μ crassi, 0.5–4 mm longi; corticati involuti, cortex paraplectenchymatous, 10–18μ crassi, biseriatus vel triseriatus cellularum; cellulae aliquantae rotundati, 4.5–7.6μ in diametro; medulla cum laxis hyphis et caveis; stratum algarum involutum, 30–60μ crassum; 1–4 cellulae algarum conventae; cellulae 12–18μ in diametro; phycobiont *Anacystis*. Lobi fertiles et steriles aequi in magnitudine; apothecia absoluta immersa in apicibus loborum, 1–3 per lobum; disci punctiformes ad 0.1 mm latum; epithecium stramineum, K ; hymenium 120–180μ crassum, ad 275μ in dimetro; paraphyses simplices, capitati, 1.8–2.4μ crassi; ascus cum vagina gelatinosa, 18–30 $\times$ 70–75μ contines 100 plus quam sporae; sporae hyalinae, simplices, globosae, 3.1–4.5μ in diametro. Hymenium I^+ vinosum-rubrum, vagina I . Pycnidia immersa in apicibus loborum, 122–214μ in diametro; conidia exobasidia, 3.1 $\times$ 0.8–1.2μ.

Thallus subfruticose (Fig. 18–19), olive-brown with growing tips lighter colored, forming continuous areas over substrate; lobes cylindrical, upright, somewhat branched, tips sometimes somewhat flattened, stalk sometimes slightly offset or flattened, very young squamules slightly peltate, surface smooth; non-sorediate, nonisidiate; attached by umbilicus. Thallus lobes 296–741μ thick, 0.5–4 mm long; corticate all around, cortex paraplectenchymatous, 10–18μ thick, 2–3 layers of cells; cells somewhat rounded, 4.5–7.6μ diameter, medulla with loose hyphae and hollow areas (Fig. 3); algal layer all around, 30–60μ thick; algae in clumps of 1–4 cells; cells 12–18μ diameter; phycobiont *Anacystis*. Fertile lobes same size as sterile lobes; apothecia totally immersed in tips of lobes, 1–3 per lobe (Fig. 6); discs punctiform to 0.1 mm wide; epithecium yellowish, K^-; hymenium 120–180μ thick, to 275μ in diameter; paraphyses simple, capitate, 1.8–2.4μ thick; asci with gelatinous sheath, 18–30 $\times$ 70–75μ, containing 100 or more spores; spores hyaline, nonseptate, globose, 3.1–4.5μ diameter. *Hymenium* I^+ wine-red, sheath I . *Pycnidia* immersed in tips of lobes, 122–214μ diameter; conidia exobasidial, 3.1 $\times$ 0.8–1.2μ.

Type: GEORGIA. DEKALB CO.: 20 miles E of Atlanta on Mt. Arabia, *Wetmore 19264*, 1969. [Holotype in my herbarium, Isotypes to be widely distributed (over 100 packets)].

TAXONOMIC REMARKS. This species is similar to *Peltula tortuosa*, but it has more terete lobes, the fertile lobes are the same size as vegetative lobes, and the ascus has a gelatinous sheath. *Peltula zahlbruckneri* is more peltate, has no



FIGURES 19–20.—19. *Peltula cylindrica* (*Wetmore 19264*). Scale divisions are 1 mm each.—20. *Peltula euploca* (*Wetmore 17394*). Scale divisions are 1 mm each.

algae in the stalk of the lobes, has shorter stalks, and the lobes are more flattened and broad.

This species was first brought to my attention by Mrs. Joan Jones as a result of her studies in the Atlanta, Georgia area. She has been kind enough to supply

me with notes on the occurrence and ecology of this lichen. Most of what follows comes from her notes supplemented by my field observations.

Peltula cylindrica has been collected on five granitic outcrops within 30 miles of Atlanta: Stone Mountain, Mount Arabia, Panola Mountain, Rollaway, and Rock Chapel outcrops (Fig. 30). It is most abundant on Mt. Arabia where it covers large areas (Fig. 10–11). The average annual precipitation in the Atlanta area is 47.14 inches. *Peltula cylindrica* grows on sloping and flat rock and is abundant in fairly steep drainage paths and shallow rock depressions. In these drainage paths it is frequently wet with runoff and dries soon after the rain. The rock depressions dry within a few days after a rain. It has not been found in places where there is a persistent seepage. It is more abundant on west and southwest slopes.

Henssen also studied some material of this species, and her comments are included under *Heppia tortuosa* (Henssen, 1970).

GEORGIA. DEKALB CO.: Mt. Arabia, *Jones,* 1969 (WETMORE), *Wetmore 19264.* Panola Mt., *Jones,* 1968 (WETMORE). Stone Mt., 14 miles E of Atlanta, *Wetmore 19262.*

Peltula euploca (Ach.) Wetm., comb. nov.

Lichen euplocus Ach., Lich. Suec. Prod. 141. 1798. *Heppia euploca* (Ach.) Vain., Acta Soc. Fauna Fl. Fenn. 49(2): 14. 1921. TYPE: Sweden, *Westring* (H, not seen.)

Endocarpon guepinii Del. *in* Duby, Bot. Gall. ed. 2. 2: 594. 1830. *Endocarpiscum guepinii* (Del. *in* Duby) Nyl., Flora 47: 487, footnote. 1864. *Dermatocarpon guepinii* (Del. *in* Duby) Tuck., Lich. Calif. 28. 1866. *Pannaria guepinii* (Del. *in* Duby) Tuck., Gen. Lich. 51. 1872. *Heppia guepinii* (Del. *in* Duby) Nyl. *in* Hue, Rev. Bot. Bull. Mens. 5: 18. 1886 (= Add. Lich. Eur. 1: 62. 1886). *Peltula guepinii* (Del. *in* Duby) Gyel., Repert. Spec. Nov. Regni Veg. 38:308. 1935. *Guepinia polyspora* Hepp, Verh. Schweiz. Naturf. Ges. 48: 85. 1864 and Bot. Zeit. 22 (Beibl.): 11. 1864. *Guepinella myriocarpa* Bagl., Nuovo Giorn. Bot. Ital. 2: 175. 1870. TYPE: France. "Ad rupes schistaceos humidos ad meridiem versos in agro Andegavensi, *Guepin.*" (Not seen.)

Heppia polyphylla B. de Lesd., Ann. Cryptog. Exot. 5(2): 113. 1932. TYPE: New Mexico. Las Vegas, Soldier's Camp, *Arsène 19910.* (Lectotype US; isotypes FH, MSC.)

Heppia dermatocarpea Räs., Anales Soc. Ci. Argent. 128: 145. 1939. TYPE: Uruguay. Montevideo, Barra, saxicola, *Herter,* 1933 (Holotype H.)

NOMENCLATURAL REMARKS. Wainio (1921) selected the material from Sweden as the type of *Lichen euplocus* Ach. I have seen photographs of this material, and the identification seems to be correct.

Guepinia polyspora Hepp was proposed as a *nomen novum* for *Endocarpon guepinii.* Hepp found that the asci contained about 100 spores and so could not remain in *Endocarpon.*

Guepinella myriocarpa Bagl. was proposed as a *nomen novum* for *Endocarpon guepinii.*

The holotype of *Heppia polyphylla* B. de Lesd. has probably been destroyed. I select the isotype in US as lectotype.

The holotype of *Heppia dermatocarpea* Räs. is identical with other monophyllous material of *Peltula euploca* from other parts of the world.

Thallus peltate (Fig. 20), tan olive-green; squamules 3–10 mm diameter, lobed and polyphyllous or only slightly notched or entire; margins thicker, down-

rolled, not undulate, sorediate; attached by umbilicus. Thallus 214–367μ thick, no upper cortex; lower cortex of several layers of rounded cells in 7–10 rows, 50–90μ thick; medulla of loose hyphae; algal layer 75–150μ thick (Fig. 2). *Apothecia* many per squamule, totally immersed; discs punctiform or expanded to 0.7 mm, no thalloid rim; epithecium yellowish-brown, K ; hymenium 105–220μ thick, often pinkish; paraphyses capitate, 1.5–3.0μ thick; asci with gelatinous sheath, 100–120 $\times$ 21–27μ, containing 100 or more spores; spores ellipsoid to fusiform, 6.0–7.6 $\times$ 3.0–4.5μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 3.4 $\times$ 1.5μ.

Peltula euploca has an Arid Southwestern distribution in North America with a few outliers (Fig. 31). It occurs on noncalcareous rock in both very dry habitats and in shady areas of rock which are probably subject to intermittent water flow (Fig. 9).

Taxonomic Remarks. Sometimes the umbilicus of this species and *P. holanderi* may begin growing after the main thallus has been broken off. In these cases the regenerated growth may resemble that of normal *P. placodizans*. Occasionally young thalli may not have well developed soralia and separation of these from *P. omphaliza* is difficult unless apothecia are present. A few pruinose specimens were seen but this species is usually epruinose.

Alabama. county unknown: Locality unknown, *Peters*, 1883 (FH).
Arizona. coconino co.: 2 miles N of Flagstaff in Rio de Flag Canyon, *Shushan & Johnson S 14851* (SHUSHAN). cochise co.: Chiricahua Mts., Stewart Campground between Portal and the forks of Cave Creek, *Weber, Shushan & Anderson S-24659* (COLO); W of Portal on trail from Rustler's Park to Fly's Peak, *Weber & Shushan S-8987* (COLO). graham co.: Coronado National Forest, above Stockton Pass Campground, S of Safford, *Wetmore 14466, 14499*. pima co.: Tumamoc Hill, west outskirts of Tucson, *Weber L-36747* (COLO). Tucson Mts., *Darrow 1309* (COLO).

Arkansas. county unknown: Ozark Mts., *Peters*, 1876 (FH).

California. county unknown: Canta Cruz Mts., *Hasse* (MICH). Mt. Hamilton Road, *Herre 75* (DS). Near Ocean View, *Houe*, 1893 (NY). alameda co.: Oakland Hills, *Bolander*, before 1870 (FH). kern co.: 2.7 miles N of Caliente, *Tavares & Brinson 1169b, 1169c* (both UC). lake co.: 2 miles S of Lucerne, along Clear Lake, *Cooke 16704* (F). los angeles co.: San Gabriel Mts., *Hasse*, 1897 (ABS); Rubio Canyon, *Kingman*, 1911 (FH). San Gabriel Canyon, *Hasse*, 1902 (POM). 2 miles N of Coldbrook Station along California 39 between Crystal Lake Campground and Azuza, *Wetmore 16780, 16798*. Santa Monica Mts., *Hasse* [6 specimens collected between 1890 and 1911] (FH, LAM, NY, POM, US); Topanga Canyon, *Hasse*, 1906 (FH); NW of Topanga in Old Topanga Canyon, 2.5 miles off Topanga Canyon Road, *Wetmore 16828*. Santa Catalina Island, *Hasse*, 1906 (FH); Silver Canyon, *Nuttall 450* (F, FH); east end of Whites Cove at headland point (Bible Peak), *Weber & Santesson L-42802* (COLO). San Clemente Island, west-trending canyon running seaward toward Lost Point, *Weber & Santesson I 42879* (COLO). marin co.: Mill Valley, *Herre*, 1930 (F, LAM); 2.5 miles SE of Stinson's Beach, *Brown*, 1942 (F, LAM). monterey co.: Monterey, *Farlow* (FH). Hastings Reservation, *Linsdale 188* (F). riverside co.: Elsinore, *Hasse*, 1888 (FH). San Jacinto Mts., at S edge of Banning, *Wetmore 14629;* above Palm Desert, *Wetmore 14584, 14594;* at west edge of Palm Springs in Chino Canyon, *Wetmore 14613;* above Soboba Hot Springs (NE of Hemet), *Wetmore 14699, 14702A*. In Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16885B, 16896*. Along California 71 a few miles NE of junction with California 79, *Wetmore 16903*. S of Riverside near Perris, *Wetmore 14725*. Palm Springs, *Hasse FN 816* (FH). san barnardino co.: Along US 66 SW of Barstow 29 miles, on Wells-Stoddard Road, *Wetmore 17023*. Joshua Tree National Monument, near Hidden Valley Campground, *Wetmore 16901*. 10 miles S of Needles, *Drouet & MacBride 4683* (F). san diego co.: W of Anza-Borrego State Park on county highway S2 between California 79 and California 78,

Wetmore 16948. San Diego, *Farlow*, 1885 (PH), *Orcutt* (FH). San Diego at "Atlantus Restaurant" in Mission Bay Park, *Wetmore 17020*. Otay, *Orcutt 124* (US). Along back road between California 94 and Chula Vista near Otay Reservoir, *Wetmore 17018*. 6.8 miles SE of Temecula on road to Pala, *Tavares & Brinson 1106a* (UC). SAN MATEO CO.: S of Pasadena, *Cain 26156* (TRTC). On rocks on sea coast, *Bolander*, 1864 or 1865 (F). Pigeon Point, *Herre* [8 speimens collected between 1932 and 1957] (F, LAM, NY, TRTC, US); lighthouse, *Shushan S-14679* (COLO, US); 1 mile S of lighthouse, *Doty 5427* (F, PH, WIS). Santa Cruz Mts. near Pt. San Pedro, *Herre 499* (DS, FH, MINN, NY, US); Stony Point, Searsville Ridge, *Herre 140* (DS, FH, MINN, NY); hills near Stanford University, *Herre 149* (MU, UC); Stevens Creek Canyon, *Herre 613* (DS, FH, MINN, MO). Searsville Lake, 6 miles from Stanford University, *Shushan 11094* (COLO). Santa Cruz, *Hasse* (MICH). Alum Rock Park, *Herre 42* (DS). SONOMO CO.: Danell Estate, Sonoma Valley, *Roderick*, 1961 (UC). 1 mile N of Santa Rosa, *Brown 439* (LAM). VENTURA CO.: Locality and collector unknown, [*Hasse?*], 1903 (FH).

COLORADO. COUNTY UNKNOWN: Locality unknown, *Brandegee* (FH, MICH, US). ALAMOSA CO.: Great Sand Dunes National Monument, 25 miles NE of Alamosa, *Shushan Sl-5294* (SHUSHAN). BOULDER CO.: Boulder Canyon, vicinity of Boulder Falls, *Weber & Persson Sl-292* (COLO), *Shushan Sl-377* (SHUSHAN). Summit of Flagstaff Mt., W of Boulder, *Weber & Imshaug S-9930* (COLO), *Wetmore 15783*. Dakota Ridge W and NW of Boulder, *Anderson S-20209* (COLO), *Anderson S-20113* (COLO); Rabbit Mt., 4 miles NE Lyons of above Little Thompson River, *Anderson S-20441* (COLO, DUKE, FH, MSC). South St. Vrain Canyon, 5.5 miles W of Lyons, *Weber, Santesson & Anderson L-41951* (COLO, WETMORE). 2.5 miles NW of Lyons along North St. Vrain Creek near mouth of canyon, *Wetmore 16205, 16221*. West base of Steamboat Mt., 2 miles NW of Lyons, *Shushan & Weber S-18591* (COLO). CONEJOS CO.: 1 mile E of Manassa, *Wetmore 17287*. EL PASSO CO.: North Cheyenne Canyon, Colorado Springs, *Jeanett*, 1913 (ABS). GRAND CO.: Rocky Mt. National Park, 1 mile E of Grand Lake, base of south slope of Mt. Enentah, *Anderson 3432* (COLO); NE of Grand Lake between Summerland Park and Cascade Falls of North Inlet, *Anderson 3240* (COLO, WETMORE). JEFFERSON CO.: Along US 6, 14 miles E of Idaho Springs in Clear Creek Canyon W of Denver, *Wetmore 16243*. Clear Creek Canyon 8 miles SE of Pinecliffe, *Shushan Sl-893* (SHUSHAN). LARIMER CO.: Dakota Ridge, 22 miles N of Ft. Collins, 2 miles SE of Table Mt., *Anderson S-20154* (COLO); 4.5 miles SW of Ft. Collins, just above Horsetooth Reservoir, *Anderson S-20291* (COLO). Rocky Mt. National Park, SW slope of Deer Mt., *Anderson 3573* (COLO); Fall River Canyon, 1 mile W of Endovalley Campground near Chasm Falls along Fall River, *Anderson 1941* (COLO). Gem Lake Trail, 2 miles NE of Estes Park, *Shushan, Anderson & Sims Sl-3345* (SHUSHAN). 0.5 mile S of Wyoming state line, just N of Virginia Dale, *Shushan Sl-90* (SHUSHAN). LOGAN CO.: 7 miles N of Westplains, 27 miles NW of Sterling, *Shushan Sl-335* (SHUSHAN).

MARYLAND. WASHINGTON CO.: Harper's Ferry, *Tuckerman*, 1852 (FH, MICH, US).

MASSACHUSETTS. NORFOLK CO.: Needham, *Tuckerman*, 1844 (FH).

MINNESOTA. RENVILLE CO.: Morton, *Fink 322* (MICH, MINN, MU).

NEVADA. CLARK CO.: Mt. Diablo baseline and meridian, Las Vegas, *LePak 11-194* (COLO). On road to Mormon Mesa, 6.5 miles N of junction with highway 91, about 14 miles W of Mesquite, *Tavares 1516a* (UC).

NEW MEXICO. BERNALILLO CO.: Arroyo San Antonio, 2 miles above junction of highway 66 and Sandia Loop Drive, *Shushan & Weber S-6852* (COLO, DUKE, FH, MSC). SAN MIGUEL CO.: Las Vegas, Soldier's Camp, *Arsène 19910* (FH, MSC, US), *19890*, (FH, US). 28 miles SW of Las Vegas, 2.5 miles W of Sands, *Shushan S-11126* (COLO). Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15152 p.p.* (sub *P. bolanderi*). SOCORRO CO.: Magdalena Mts., just S of highway 5 miles SW of Socorro, *Shushan & Weber S-6927* (COLO, FH, MSC, US, WIS, WTU). UNION CO.: 3 miles N of Capulin Mt. National Monument, *Wetmore 17394*. 7 miles E of Folsom, *Shushan S-11435* (COLO).

SOUTH DAKOTA. MEADE CO.: 2.5 miles E of Piedmont Butte, 23 miles ESE of Lead, *Wetmore 10369* (MSC, WETMORE). PENNINGTON CO.: Along Pine Creek at head of Horse Thief Lake, 18 miles SW of Rapid City, *Wetmore 10962* (MSC).

TEXAS. BREWSTER CO.: Big Bend National Park, South Rim Trail to Emory Peak, Chisos Mts., *Anderson & Shushan S-18693* (COLO); Boulder Meadows, *Wetmore 18492*; Grapevine Hills NW of Headquarters, *Wetmore 18287A, 18293A*; Green Gulch, *Wetmore 18437B*; Pine Canyon, *Wetmore 18422*.

UTAH. WASHINGTON CO.: 8 miles E of St. George on west bank of Virgin River, *Shushan S-14606* (COLO). 0.5 mile E of Santa Clara along US 91, *Wetmore 17079*.

WASHINGTON. KITTITAS CO.: 20 miles NW of Wymer, *James*, 1969 (WETMORE).

Specimens also seen from Mexico, Argentina, Uruguay, Hawaii, Australia, and Europe.

Peltula michoacanensis (B. de Lesd.) Wetm., comb. nov.

Heppia michoacanensis B. de Lesd., Lich. Mexique 10. 1914. TYPE: Mexico. État de Michoacán, Morelia, lomas à l'ouest du Zapote, *Arsène 3813*, 1910. (Lectotype US; isotypes DUKE, FH, WIS).

NOMENCLATURAL REMARKS. The holotype has probably been destroyed, so I am selecting the isotype in US as lectotype.

Thallus squamulose (Fig. 21), tan-olive; squamules 1–2 mm diameter, shallowly or deeply lobed, concave and cone shaped; margins ascending; attached by central branched umbilicus. Thallus 150–350μ thick; upper cortex not developed; lower cortex of 3–5 layers of rounded cells, 25–50μ thick; medulla variable but usually cellular at lobe margins and with agglutinate hyphae in center near umbilicus with some loose hyphae; algal layer 73–130μ thick, algal cells in vertical rows. *Apothecia* one per squamule, immersed in center of concave squamule; discs 0.5–1 mm diameter, without thalloid rim, not filling squamule; epithecium light brown, K ; hymenium 150–220μ thick; paraphyses 1.7μ thick; asci with gelatinous sheath, containing 100 or more spores; spores ellipsoid to fusiform, 6.1–7.7 $\times$ 3.4–4.6μ. *Hymenium* I^+ wine-red. *Conidia* bacilliform, 3.1–3.7 $\times$ 1.2–1.8μ.

This species is very rare north of Mexico but probably much more abundant in Mexico (Fig. 32). It grows on a thin layer of soil over calcareous or non-calcareous rock.

TAXONOMIC REMARKS. The squamules are larger and cone-shaped in this species as opposed to the smaller, flat or convex squamules in *P. obscurans* var. *deserticola*. The umbilicus in *P. michoacanensis* is much larger.

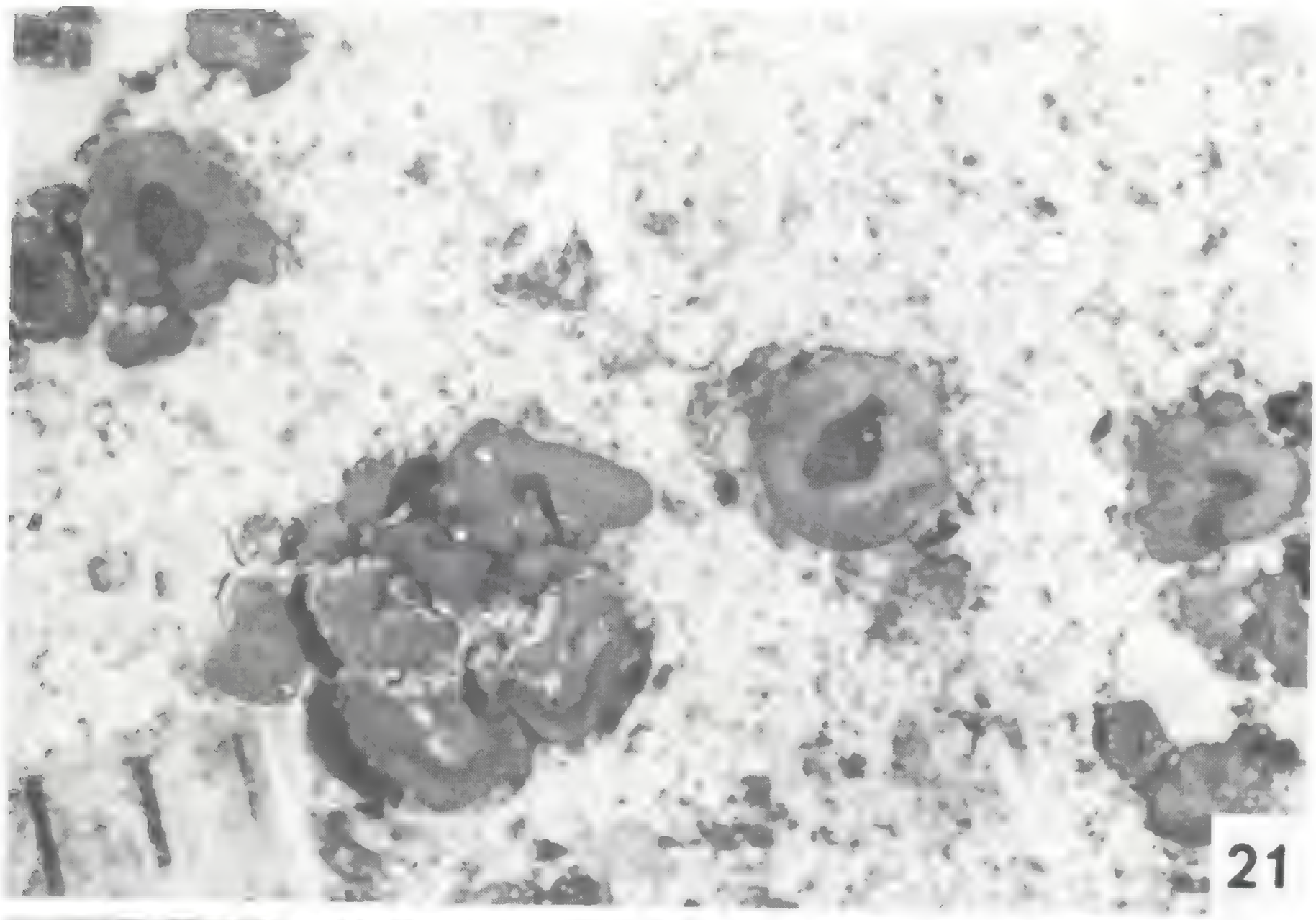
CALIFORNIA. RIVERSIDE CO.: San Jacinto Mts., above Palm Desert, *Wetmore 14595*; above Soboba Hot Springs, NE of Hemet, *Wetmore 14704*.

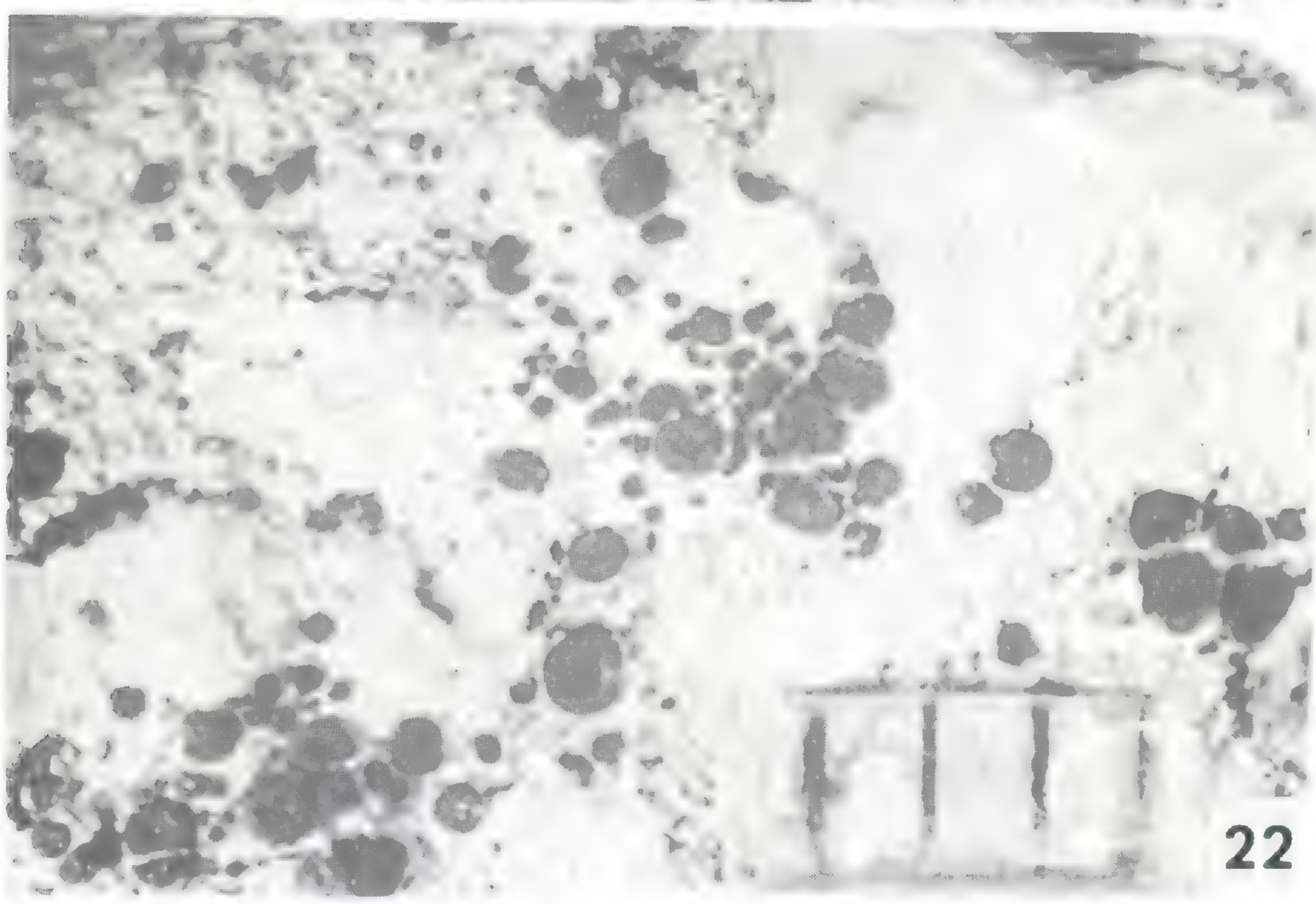
Specimens also seen from Mexico and one from India which may belong to this species.

Peltula obscurans (Nyl.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 308. 1935.

Endocarpiscum obscurans Nyl., Bull. Soc. Linn. Normandie II. 6: 309. 1872. *Heppia obscurans* (Nyl.) Nyl. *in* Hue, Rev. Bot. Bull. Mens. 5: 18. 1886 (= Add. Lich. Eur. 1: 62. 1886). *Heppia guepinii* var. *obscurans* (Nyl.) Boist., Nouv. Fl. Lich. 2: 87. 1903. TYPE: France. Collioure, *Nylander*, 1872 (Lectotype H-NYLANDER, Herb. 30900).

Heppia deserticola f. *minor* Zahlbr., Ann. Mycol. 7: 474. 1909. TYPE: Arizona. Tucson, on rocks, *Blumer*, 1908. (Holotype not found; isotypes MICH, MU).





FIGURES 21–22.—21. *Peltula michoacanensis* (*Wetmore 14595*). Scales divisions are 1 mm each.—22. *Peltula obscurans* var. *deserticola* (*Wetmore 15141*). Scale divisions are 1 mm each.

NOMENCLATURAL REMARKS. Among the original collections in Nylander's herbarium in Helsinki are two that could be considered for the types. One of these (H-NYL 30900) agrees well with the type description, and I have selected it as lectotype. The other (H-NYL 30897) was selected by Gyelnik (1935) as

lectotype, but the collection I saw from Helsinki has nothing like this species in it and is all *Peltula euploca*.

The holotype of *Heppia deserticola* f. *minor* Zahlbr. could not be found in Vienna. Since it may be found in another herbarium, I have not selected a lectotype but based the identification on the isotypes.

Taxonomic Remarks. This is a very variable species. The cortical development and the type of medulla vary somewhat with the pH of the substrate. Specimens from calcareous substrates have less well developed cellular tissues than those from noncalcareous substrates, and lobing of the thallus is more pronounced on noncalcareous substrates. Since there are a few rare intermediates between the otherwise distinct types, I have recognized the following varieties based on thallus variations and epithecium reactions.

Peltula obscurans var. **obscurans**

Thallus squamulose, brownish-olive to greenish-olive; squamules 0.2–2 mm diameter, lightly to deeply lobed, flat to convex; attached by branched umbilicus. Thallus 183–244μ thick; upper cortex not developed; lower cortex usually present but not distinguishable from the medulla; medulla cellular or rarely with loose hypae; algal layer 91–183μ thick. *Apothecia* one per squamule, at first immersed but finally emergent with thin thalloid rim; disc 0.3–0.8 mm diameter; epithecium yellowish-brown, K$^+$ red-violet; hymenium 70–150μ thick; paraphyses 1.5–3.0μ thick; asci with gelatinous sheath, 52–75 $\times$ 15–18μ, containing 100 or more spores; spores ellipsoid to oval, 4.5–7.6 $\times$ 3.0μ. *Hymenium* I$^+$ wine-red. *Conidia* oval-fusiform, 3.1–3.7 $\times$ 1.2μ.

This variety probably has an Arid Southwestern distribution but has only been found along the southern border of the United States (Fig. 33). It will probably be found in Mexico after more collecting is done there. It usually grows on rock but occasionally on soil. The substrates are usually noncalcareous. It grows in open, dry, rocky deserts.

Taxonomic Remarks. The lectotype collection of the species has the K$^+$ red reaction in the hymenium. This variety has thallus variations similar to the other varieties but has the K$^+$ red-violet epithecium. This is the rarest variety in spite of being the typical variety nomenclaturally.

Exsiccati: *Plitt, Lich. Exs.* 35 (sub *Heppia hassei*) (ABS, F).

Arizona. cochise co.: Chiricahua Mts., Cave Creek Canyon, 3 miles N of Portal, *Weber & Shushan* S 8839 (COLO). maricopa co.: N of Gila Bend on US 80, *Wetmore 14533A*. pima co.: Tucson, *Blumer*, 1908 (MICH, MU), *Darrow* 572 (COLO). Saguaro National Monument, NW of Tucson, *Wetmore 14514A, 14518B*.

California. los angeles co.: Santa Monica Range, *Hasse*, 1902 (US), 1908 (ABS). Santa Monica Hills near Sawtelle, *Hasse*, 1908 (F). riverside co.: San Jacinto Mts., above Palm Desert, *Wetmore 14577*. Palm Springs, *Hasse*, 1903 (NY, POM), 1904 (MICH).

Nevada. clark co.: 14 miles W of Mesquite, on road to Mormon Mesa, *Tavares 1509, 1516d* (both UC).

New Mexico. dona ana co.: Organ Mts., 15 miles E of Las Cruces near San Agustin Pass along US 70, *Wetmore 14442B*.

Texas. brewster co.: Big Bend National Park, Green Gulch, *Wetmore 18445;* 2 miles from highway on road to Grapevine Hills, *Wetmore 18294A*. upton co.: North of McCamey in King Mt. area, *Wetmore 14240*.

Specimens also seen from Mexico, Peru, France, and Italy.

Peltula obscurans var. **deserticola** (Zahlbr.) Wetm., comb. nov.

Heppia deserticola Zahlbr., Bull. Torrey Bot. Cl. 35: 300. 1908. TYPE: Arizona. Tucson, southward facing tuff, station III, *Blumer,* 1908. (Holotype not found; isotype MICH.)

Heppia michoacanensis var. *adnata* B. de Lesd., Lich. Mexique, 1 Suppl. 8. 1922, processed publication. TYPE: Mexico. Michoacán, Azotea de San Borja, Arsène 9604, 1914. (Lectotype US; isotype DUKE.)

NOMENCLATURAL REMARKS. The holotype of *Heppia deserticola* Zahlbr. could not be found in Vienna, but since it may later be found I have not selected a lectotype. I have based my interpretation on the isotype.

Heppia michoacanensis var. *adnata* B. de Lesd. was described in a mimeographed paper and so was not validly published. I have not found a later valid publication. The holotype has probably been destroyed, and I am selecting the isotype in US as the lectotype.

Thallus squamulose (Fig. 22), olive-brown; squamules 0.5–1.2 mm diameter, not lobed or only slightly so, convex or flat; attached by clump of rhizines or umbilicus. Squamules 105–240μ thick; upper cortex not developed; lower cortex poorly developed or not present; medulla of loose hyphae or with rare cellular areas; agal layer 60–120μ thick. *Apothecia* one or two per squamule, immersed and finally filling the whole squamule leaving squamule margin as the rim (Fig. 5); disc 0.3–1.2 mm diameter, epithecium yellowish-brown, K^-; hymenium 105-140μ thick; paraphyses 1.5–3.0μ thick; asci with gelatinous sheath, 60–75 $\times$ 19–27μ, containing 100 or more spores; spores ellipsoid to oval, 4.6–7.7 $\times$ 3.0–4.6μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 3.1–3.7 $\times$ 1.2–1.8μ.

This variety has an Arid Southwestern distribution (Fig. 34) and is very abundant in dry semi-desert and desert areas (Fig. 14). In many areas it occurs on almost all pebbles in the area, however, since it is small, it has been rarely collected. It usually occurs on calcareous rock.

TAXONOMIC REMARKS. The degree of development of the cellular tissue of the thallus is better on noncalcareous rocks. See further notes under the species.

Exsiccati: *Plitt, Lich. Exs. 138* (sub *Heppia holanderi*) (DS).

ARIZONA. COCHISE CO.: Near Portal, E of Chiricahua Mt. base, *Roth,* 1963 (COLO). COCONINO CO.: Grand Canyon, Bright Angel Trail, *Hasse,* 1904 (NY); South Rim, Hermit's Rest trail, *Wetmore 14985B, 14986*; South Rim, Rowes Well Road, *Wetmore 15016*. 25 miles S of Grand Canyon on US 180, *Wetmore 14932*. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14532*. Sauceda Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14542*. Pinnacle Peak Pass, 4 miles from Verde River near Scottsdale, *Weber & McCleary S-1929* (COLO). NAVAJO CO.: 10 miles E of Winslow on US 66, *Wetmore 15045*. PIMA CO.: Tucson, *Blumer,* 1908 (MICH, MU). Tumamoc Hill, west outskirts of Tucson, *Weber L-36749, L-37649, L-36755* (all COLO, WETMORE). Tucson Mts., *Darrow 746* (WIS). Saguaro National Monument NW of Tucson, *Wetmore 14514C*. Near Pantano, SW of Tucson on US 80, *Wetmore 14511, 14512*. Organ Pipe Cactus National Monument below headquarters. *Sierk 2285* (SIFRK). PINAL CO.: Picacho Pass NW of Tucson along Interstate 10, *Wetmore 14520, 14522*. YAVAPAI CO.: 6 miles W of Ash Fork on US 66, *Wetmore 14924*. Along Arizona 279 SE of Cottonwood, *Wetmore 15041*. YUMA CO.: Near Mohawk E of Yuma on US 80, *Wetmore 14546*.

CALIFORNIA. INYO CO.: Death Valley National Monument, NE of Stovepipe Wells, *Wetmore 14879*. LOS ANGELES CO.: Santa Monica Mts., *Hasse FN 917* (FH), 1915 (DS); Sullivan's Canyon, *Hasse,* 1913 (FH); Topanga Canyon at "4 Oaks," *Hasse* (FH). Catalina

Island, *Hasse FN 1400* (FH) 1911 (FH). RIVERSIDE CO.: S of Cathedral City, *Wetmore 16870*. Near western edge of Palm Desert, *Wetmore 16851*.

COLORADO. BOULDER CO.: Between Altona and Lyons, 0.5 mile S of Summit Red Hill, *Shushan & Weber 3368* (COLO). West base of Steamboat Mt., 2 miles NW of Lyons, *Shushan & Weber S-17936* (COLO). 1.5 miles NW of Lyons on Steamboat Mt., *Wetmore 16125, 16173, 16176A, 16182*.

KANSAS. CHASE CO.: Locality unknown, *Hall 14* (FH).

NEVADA. CLARK CO.: Along US 91 NE of Las Vegas, 22 miles at road going to Axial, *Wetmore 17042*. Near Gold Butte, *Tavares 31f* (UC). Virgin River, 2.5 miles NE of Mesquite, *Tavares 473a* (UC). Road to Mormon Mesa, 14 miles from Mesquite, *Tavares 1253, 1507, 1516* (UC). NYE CO.: Near Mercury, along US 95, *Wetmore 14889A*.

NEW MEXICO. EDDY CO.: Near Hope, 21 miles W of Artesia along US 82, *Wetmore 14319B, 14321*. LUNA CO.: Near Gage, 19 miles W of Deming on US 70, *Wetmore 14459*. MCKINLEY CO.: Along US 66 at road to Manvelito, 13 miles W of Gallup, *Wetmore 15065, 15090*. SAN DOVAL CO.: N of Albuquerque on road to Placitas, *Wetmore 15141*, 15142. SAN MIGUEL CO.: Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15169*.

OKLAHOMA. GARFIELD CO.: 3 miles SW of Douglas by Wolf Creek, *Keck 268* (KECK). MURRAY CO.: Platt National Park, *Wetmore 14122B*. TEXAS CO.: 7 miles NE of Guyman on US 54, *Wetmore 15225*.

TEXAS. BREWSTER CO.: Big Bend National Park, below Burro Mesa Pouroff, *Wetmore 18312B;* Dagger Flats, *Wetmore 18208;* 2 miles W of junction with road to Castolon, *Wetmore 18302;* Grapevine Hills NW of headquarters, *Wetmore 18288;* 2 miles from highway on road to Grapevine Hills, *Wetmore 18294B;* Green Gulch, *Wetmore 18430;* Hot Springs near Rio Grande Village, *Wetmore 18187, 18192;* 4 miles W of junction of main road and road to Basin Campground, *Wetmore 18295A;* Old Mine Road near Rio Grande Village, *Wetmore 18379;* 7 miles W of junction with road to Basin Campground, *Wetmore 18296;* W of junction going to Santa Elena Canyon along Texas 170, *Wetmore 14304, 14307;* at junction of US 385 and Texas 2627, 40 miles from Park headquarters, *Wetmore 14246*. BROWN CO.: SW of Brownwood on US 67, *Wetmore 14217*. UPTON CO.: N of McCamey in King Mt. area, *Wetmore 14232*.

UTAH. EMERY CO.: Along US 6, 27 miles S of Price, *Wetmore 16519A*. GRAND CO.: Along US 6, 2 miles E of Green River, *Wetmore 16503*.

Specimens also seen from Mexico.

Peltula obscurans var. **hassei** (Zahlbr.) Wetm., comb. nov.

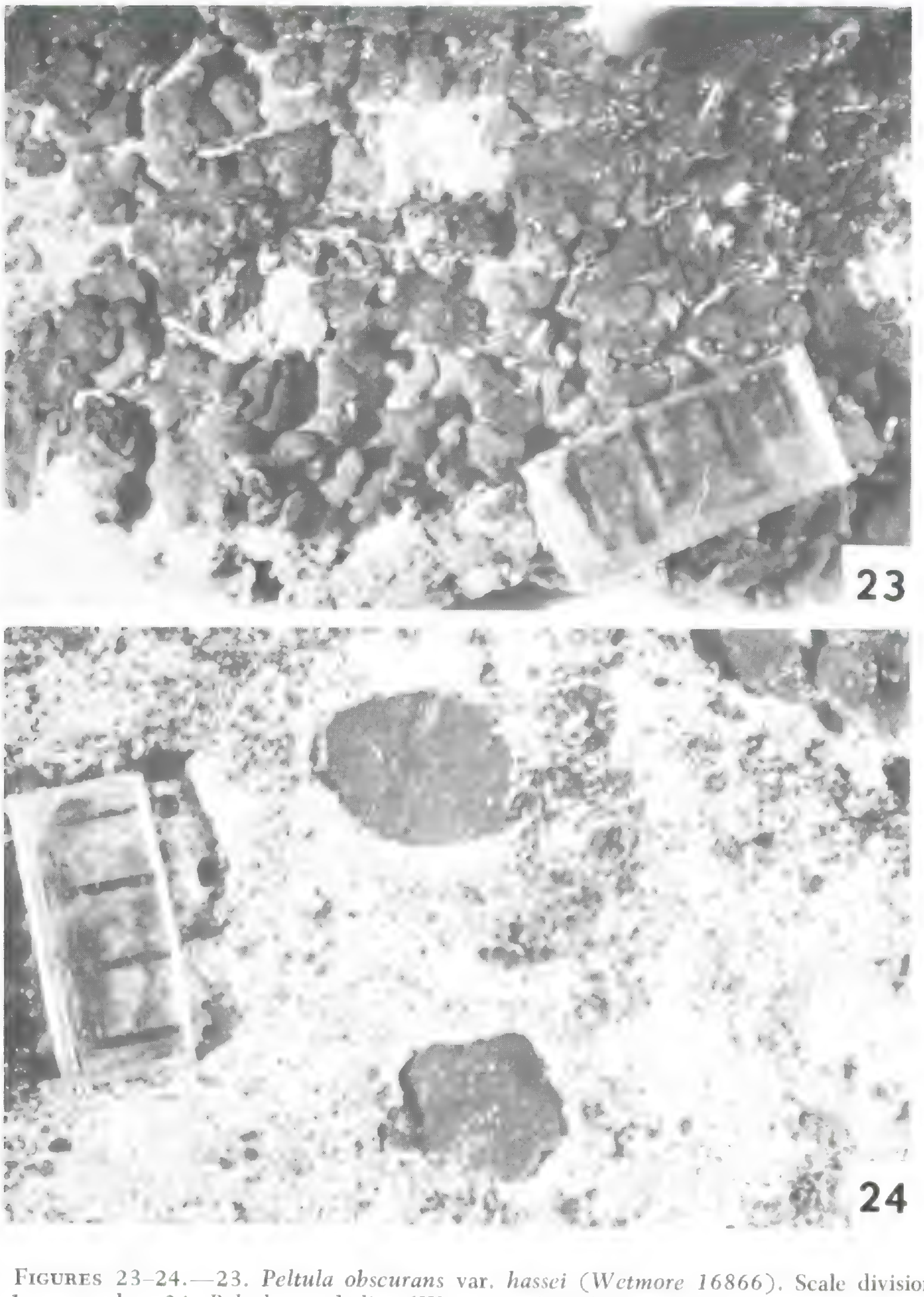
Heppia hassei Zahlbr., Beih. Bot. Centrbl. 13: 157. 1902. TYPE: California. Palm Springs, ad saxa granitica, *Hasse FN 817*. (Lectotype W.) *Hasse FN 827*. (Syntype FH, NY).

Heppia murorum Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 218. 1890 (= Étude Lich. Brésil 1: 218. 1890). TYPE: Brasil. Rio de Janeiro, ad cementum muri, *Wainio, Lich. Brasil. Exs. 190*. (Holotype not seen; isotype FH.)

NOMENCLATURAL REMARKS. Zahlbruckner cited two collections in the original description of *Heppia hassei*. Only *Hasse Field Number 817* remains in Vienna, and I am selecting this as lectotype. The lectotype packet also contains another species of Heppiaceae with a K^+ red epithecium and loose medulla. I have marked the thallus to be used as the lectotype for var. *hassei*, but the other species needs further study.

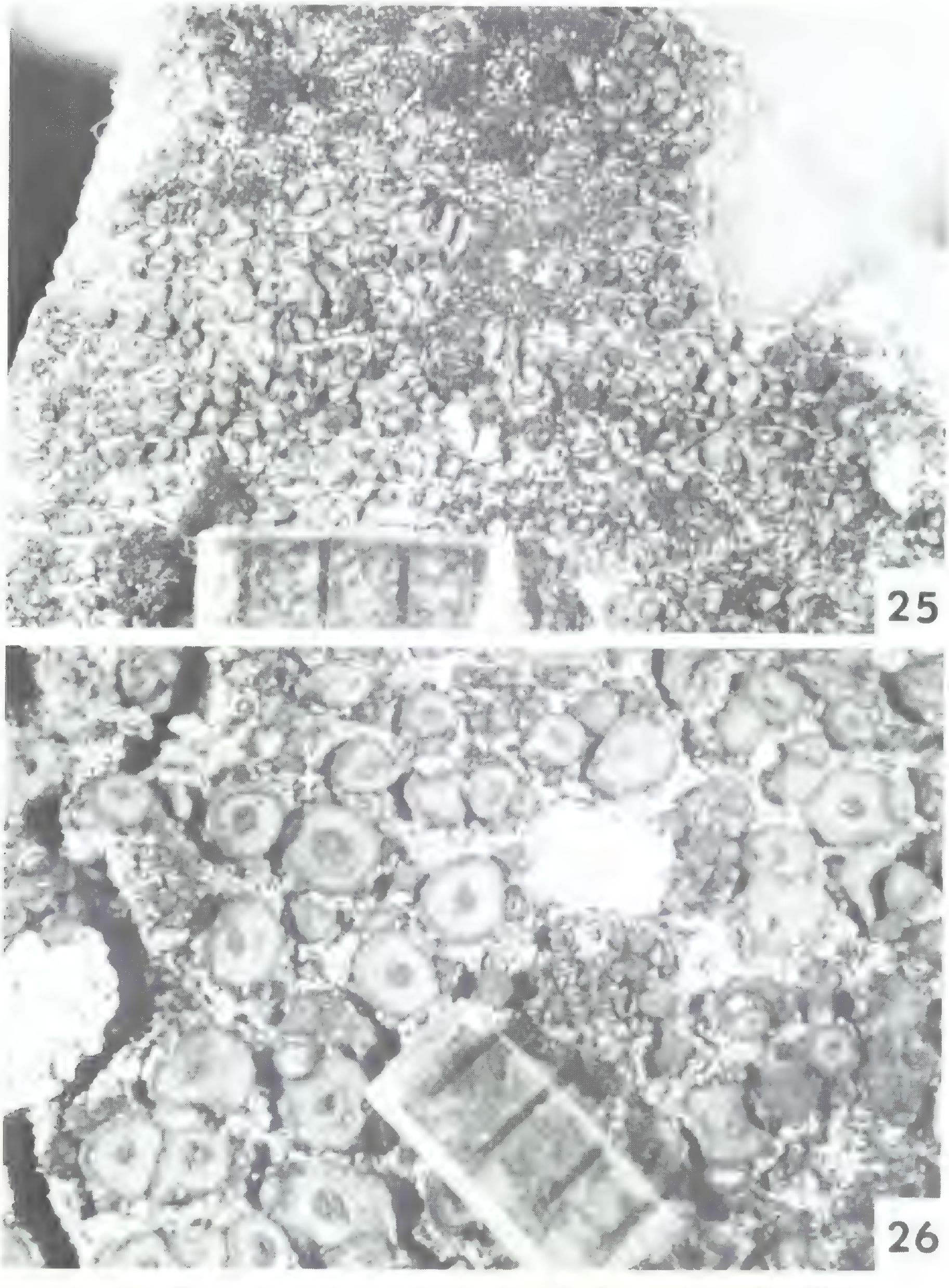
Heppia murorum Wain.—See below under taxonomic remarks.

Thallus squamulose (Fig. 23), brown to olive-brown; squamules usually deeply lobed and polyphyllous, squamules 1–2 mm diameter, attached by tuft of rhizines or branched umbilicus. Squamules 122–210μ thick; upper cortex not developed; lower cortex cellular like medulla but with thicker cell walls, 15–22μ thick; medulla cellular but with occasional areas of loose hyphae; algal layer



FIGURES 23–24.—23. *Peltula obscurans* var. *hassei* (*Wetmore 16866*). Scale divisions are 1 mm each.—24. *Peltula omphaliza* (*Wetmore 17045*). Scale divisions are 1 mm each.

45–90μ thick. Apothecia 1(–3) per squamule, at first immersed but later emergent with thalloid rim; discs 0.5–1.0 mm diameter, sometimes filling whole squamule lobe; epithecium yellow-brown, K ; hymenium 120–150μ thick; paraphyses 1.5–3.0μ thick; asci with gelatinous sheath, 60–68 $\times$ 12–18μ, containing 100 or more spores; spores oval, 6–7.6 $\times$ 3–4.5μ *Hymenium* I$^+$ wine-red. *Conidia* oval to fusiform, 3.1–4.3 $\times$ 1.8–2.4 (–3.1)μ (Fig. 8).



FIGURES 25–26.—25. *Peltula placodizans* (*Wetmore 18491*). Scale divisions are 1 mm each.—26. *Peltula polyspora* (*Wetmore 14707*). Scale divisions are 1 mm each.

This variety has an Arid Southwestern distribution (Fig. 35) and in some localities may be fairly abundant. It usually grows on noncalcareous rock but also sometimes on calcareous rock and on soil in rock cracks.

TAXONOMIC REMARKS. Some collections have varying amounts of loose hyphae in the medulla, but this development is always less than in var. *deserticola*.

Sometimes with different sections of the thallus different amounts of cellular development are found. The specimens on hard granite are usually less lobed. See further remarks under the species.

The isotype of *H. murorum* (FH) seems to be this variety, but it is too small to be sure. Lamb (notes in FH) confirms that *Placodium subglebosum* Müll.-Arg. is the same as *H. murorum,* but I have not seen any of the original material of the *Placodium.* If these are identical, the correct epithet for this taxon, when treated as a species, would have to be *subglebosum.* This synonymy is not made here pending study of the holotypes.

The name *Heppia conchiloba* Zahlbr. has been misapplied to this taxon in North America, but the type of *H. conchiloba* is *H. lutosa.*

Exsiccati: *Plitt, Lich. Exs.* 35 (FH), *139* (sub *Heppia polyspora*) (DS, MU), *238* (sub ***Heppia conchiloba***) (ABS, F, FH, MU).

ARIZONA. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14534A.* Gila Bend, *Hasse,* 1898 (NY). Sauceda Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14539B, 14543B.* MOHAVE CO.: 27 miles E of Kingman near Hackberry along US 66, *Wetmore 14912.* PIMA CO.: Sierra Tucson, *Pringle,* 1884 (FH, MICH, US). Tumamoc Hill, west outskirts of Tucson, *Weber L-36750* (COLO). Saguaro National Monument NW of Tucson, *Wetmore 14516A.*

CALIFORNIA. COUNTY UNKNOWN: Hasse (FH, MICH). KERN CO.: 2.7 miles N of Caliente, *Tavares & Brinson 1156B* (UC). E of Maricopa on California 166, *Wetmore 14799.* LOS ANGELES CO.: Santa Monica Mts., *Hasse* [14 collections made between 1898 and 1911] (ABS, DS, F, FH, MICH, MU, NY, US). Topanga Pass, *Hasse,* 1909 (US), 1908 (FH). San Gabriel Mts., Rubio Canyon, *collector unknown,* 1911 (FH). San Clemente Island, between Eel Point and Seal Cove, west shore of island, *Weber & Santesson L-42663* (COLO). RIVERSIDE CO.: Elsinore, *Hasse,* 1898 (FH, NY, US). S of Cathedral City, *Wetmore 16865, 16866, 16869.* San Jacinto Mts., above Palm Desert, *Wetmore 14575, 14583B, 14585B, 14600, 14601C.* Near western edge of Palm Desert, *Wetmore 16837B, 16841, 16842, 16843, 16844, 16852, 16853.* Palm Springs, *Hasse FN 817* (W), *FN 827* (FH, NY), [7 collections made between 1901 and 1903] (FH, MINN, NY, POM). San Jacinto Mts. at western edge of Palm Springs in Chino Canyon, *Wetmore 14622B, 14624B.* Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16878, 16885A, 16892, 16899A, 16900.* Along California 71 a few miles NE of junction with California 79, *Wetmore 16902, 16919, 16924, 16926.* Eden Hot Springs, *Hasse,* 1911 (FH, US). West edge of San Jacinto Mts. above Soboba Hot Springs, NE of Hemet, *Wetmore 14692B, 14693A, 14701B, 14713, 14721.* S of Riverside near Perris, *Wetmore 14726.* Along US 66 SW of Barstow, 29 miles on Wells-Stoddard Road, *Wetmore 17030.* SAN DIEGO CO.: One mile NW of Descanso, N of US 80, *Wetmore 16962.* SANTA BARBARA CO.: Near Santa Barbara, *Hasse,* 1903 (LAM). SANTA CLARA CO.: Alum Rock Park, *Baltzo,* 1968 (UC). SONOMA CO.: Santa Rosa, *Brown,* 1946 (F). VENTURA CO.: Matilija Canyon, *Hasse,* 1903 (FH). 6.7 miles N of Santa Paula on California 150, *Tavares 1270a* (UC).

NEW MEXICO. COUNTY UNKNOWN: *Greene,* 1880 (US). VALENCIA CO.: Along San Jose River, 3.5 miles SE of Correo on road to Las Lunas, *Shushan & Weber S-6876* (COLO).

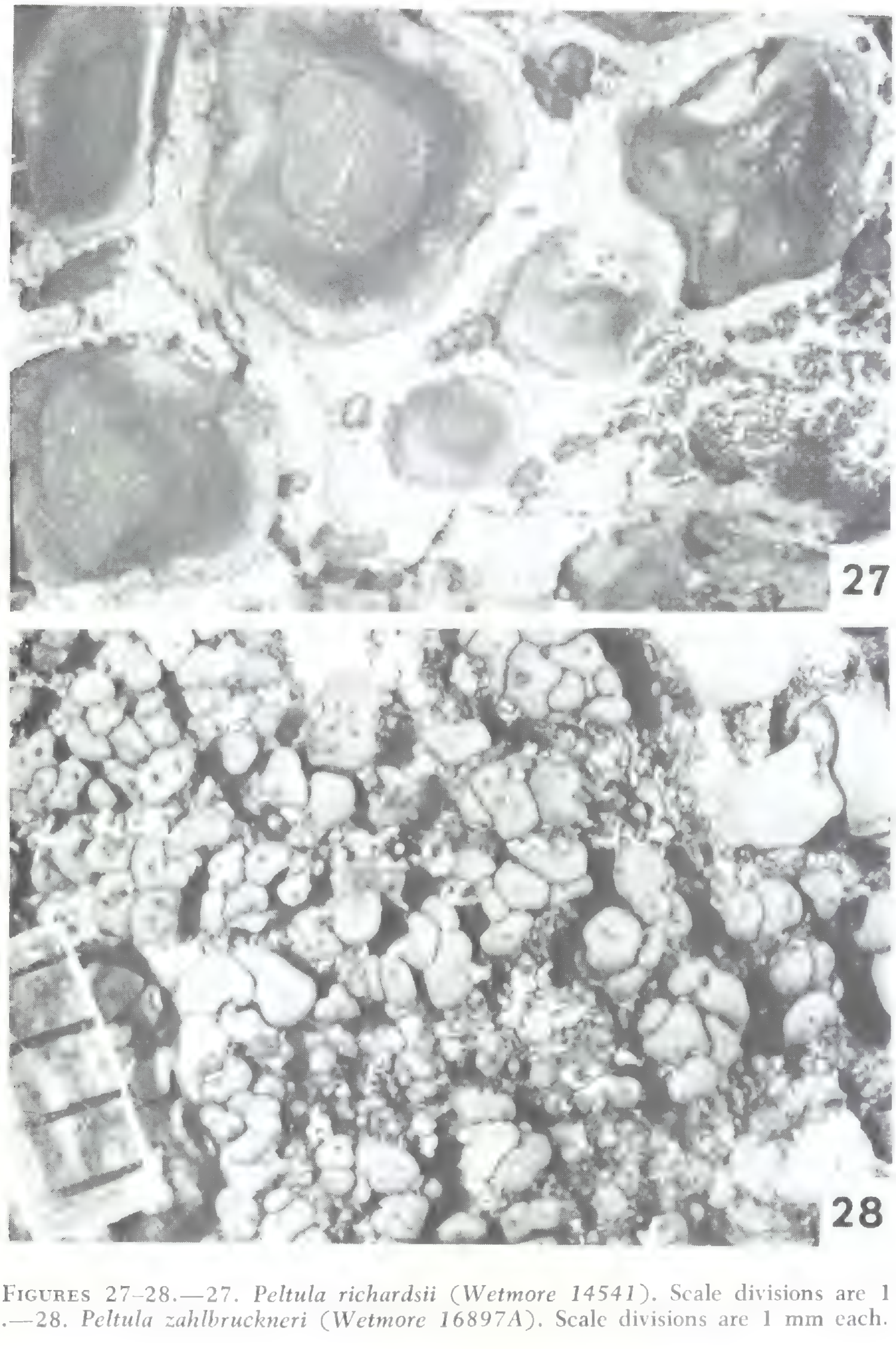
TEXAS. BREWSTER CO.: Big Bend National Park, along Lost Mine Trail from Panther Pass, *Wetmore 14265A;* Pulliam Ridge, *Wetmore 18203B.*

Specimens also seen from Mexico, Brazil, France, and Italy.

Peltula omphaliza (Nyl. *in* Eckf.) Wetm., comb. nov.

Heppia omphaliza Nyl. *in* Eckf., Bull. Torrey Bot. Cl. 16: 106. 1889. *Endocarpiscum omphalizum* (Nyl. *in* Eckf.) Müll.-Arg., Hedwigia 34: 28. 1895. TYPE: Mexico. Gulf of California, island of San Pedro Martin, *Palmer,* 1887. (Holotype H-NYLANDER 30893; isotypes F, PH, US.)

NOMENCLATURAL REMARKS. The holotype is in Nylander's herbarium, but duplicates were found in several other herbaria with varying label data. Some



FIGURES 27–28.—27. *Peltula richardsii* (*Wetmore 14541*). Scale divisions are 1 mm each.—28. *Peltula zahlbruckneri* (*Wetmore 16897A*). Scale divisions are 1 mm each.

of the labels even have Eckfelt as the collector. All of the rocks are of the same type and the associated lichens are the same on all pieces. I am confident that the errors in labeling are due to the practices used in distribution of the duplicates.

Thallus peltate (Fig. 24), greenish-olive to brownish; squamules 0.5–3 (–4) mm diameter, roundish and convex or slightly lobed and flat; margin finely

wavy; attached by umbilicus. Squamules 153–275μ thick; upper cortex not developed; lower cortex of 3–5 layers of cells, 24–36μ thick; medulla of loose hyphae; algal layer 90–120μ thick. *Apothecia* 5–20 per squamule, totally immersed; disc at first punctiform, later slightly expanded, 0.1–0.2 mm diameter, without thalloid rim; epithecium yellow to yellowish-brown, K^+ red-violet or K ; hymenium 120–150μ thick; paraphyses 1.5–2.4μ thick; asci with gelatinous sheath, 60–75 × 16–23μ, containing 100 or more spores; spores ellipsoid to bacilliform 4.6–6.1 × 3.0μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 2.4–3.1 × 1.2μ.

Peltula omphaliza has an Arid Southwestern distribution (Fig. 36) and will probably be found in many more localities in Mexico. It grows on both calcareous and noncalcareous rock in open exposed areas.

TAXONOMIC REMARKS. The epithecium reaction with K is variable even on the same thallus. Probably the reaction is basically K^+, but sometimes the substance is in low concentration or destroyed by preservation treatments. When the thallus is young it is roundish and convex, but with age and growth it becomes flat and slightly lobed.

ARIZONA. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14533B*. Sauceda Mts., 14 miles S of Gila Bend on Ariz. 85, *Wetmore 14543E*. PIMA CO.: Tumamoc Hill, west outskirts of Tucson, *Weber L 36753* (COLO). Saguaro National Monument NW of Tucson, *Wetmore 14514B, 14515A*.

CALIFORNIA. LOS ANGELES CO.: Santa Monica Mts., *Hasse* (FH). Santa Catalina Island, headland between Cottonwood Canyon and Mills Landing, *Weber & Santesson L-42790* (COLO). RIVERSIDE CO.: Near western edge of Palm Desert, *Wetmore 16850*. Palm Springs, *Hasse FN 901* (FH). Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16897B*. SAN DIEGO CO.: One mile NW of Descanso north of US 80, *Wetmore 16959A, 16968*.

NEVADA. CLARK CO: Along US 91 NE of Las Vegas, 22 miles on road going to Axial, *Wetmore 17044A, 17045*. On road to Mormon Mesa, 14 miles W of Mesquite, *Tavares 1516b, 1516c* (both UC).

TEXAS. BREWSTER CO.: Big Bend National Park, below Burro Mesa Pouroff, *Wetmore 18312A;* 4 miles W of junction of main road and road to Basin Campground, *Wetmore 18295C*. CULBERSON CO.: 22 miles S of Van Horn, *Anderson & Shushan Sl-8836* (COLO).

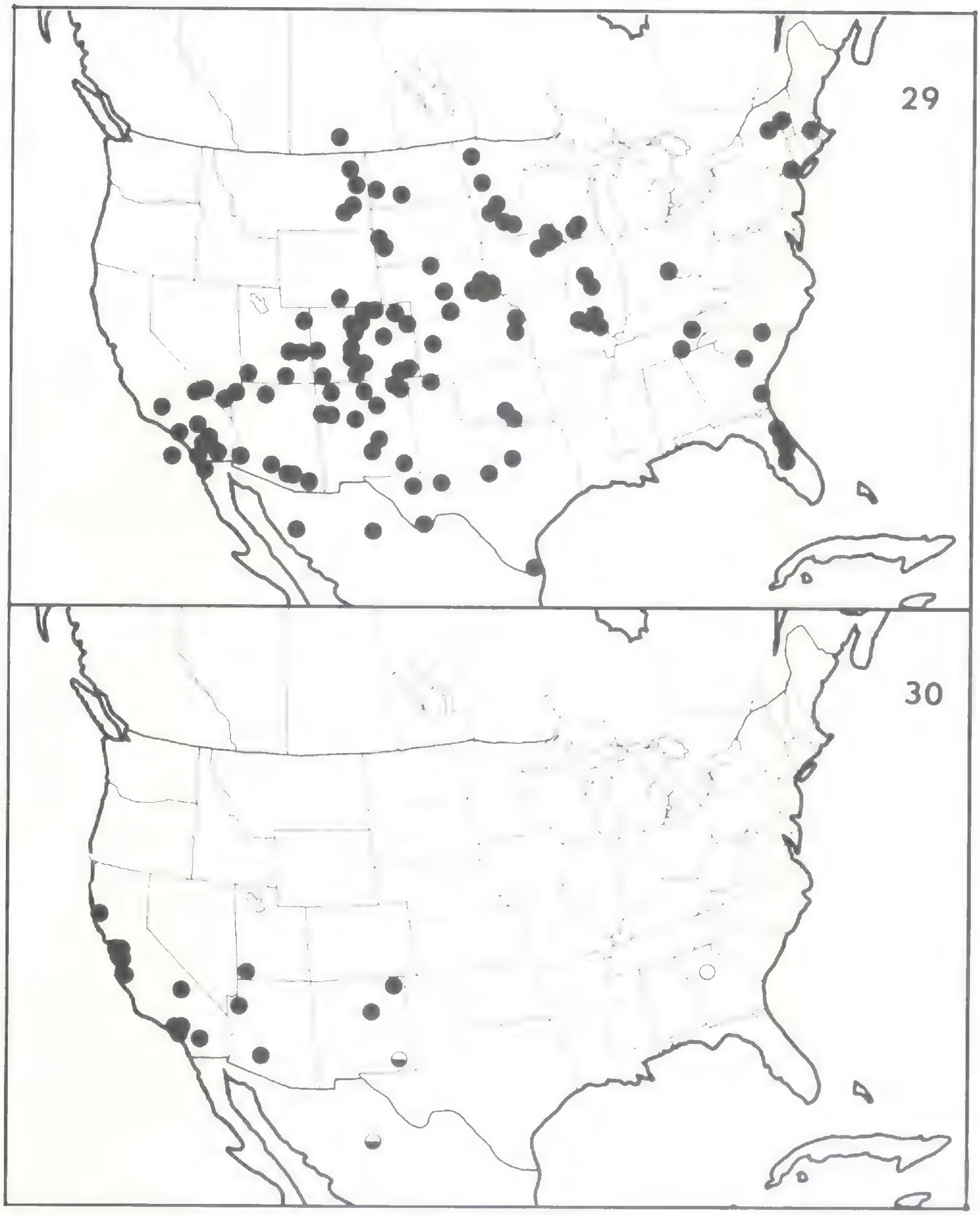
Specimens also seen from Mexico, Equador, France, and Italy.

Peltula placodizans (Zahlbr.) Wetm., comb. nov.

Heppia placodizans Zahlbr., Bull. Torrey Bot. Cl. 35: 299. 1908. *Endocarpiscum placodizans* (Zahlbr.) Fink, Mycologia 1: 87. 1909. *Solorinaria placodizans* (Zahlbr.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. *Placoheppia placodizans* (Zahlbr.) Oksn., Fl. Lich. Ucrain. 1: 407. 1956, *comb. inval.* (no basionym cited). TYPE: Arizona. Tucson, Tumamoc Hill, station II, southward facing cliff of boulders, 2600 ft., *Blumer,* 1908. (Holotype W; isotypes DS, FH, MICH.)

NOMENCLATURAL REMARKS. The label data is incomplete on several of the isotype collections and the holotype, but the collection in DS has complete data and the rock chip fits perfectly onto the rock in Vienna!

Thallus areolate-placodiform (Fig. 25), brownish to olive-green, 2–8 mm diameter, lobate at margins, areolate in center; lobes 0.2–0.5 mm wide, to 1.3



FIGURES 29–30. The distribution of North American Heppiaceae.—29. *Heppia lutosa*. —30. *Peltula bolanderi*, closed circle; *P. clavata*, half-closed circle; *P. cylindrica*, open circle.

mm long, branched, flat to convex, not inflated; central areoles roundish; whole thallus adnate to substrate, no rhizines or umbilicus apparent; areoles with capitate soralia on upper surface; soredia black, farinose. Thallus 150–244μ thick; upper cortex not developed; lower cortex like medulla; medulla cellular;

algal layer 75–90μ thick. *Apothecia* one per areole, immersed; disc at first punctiform later to 0.3 mm diameter, without thalloid rim; epithecium yellowish-brown, K^+ or K^-; hymenium 90–120 (–165)μ thick; paraphyses 1.5-3.0μ thick; asci with gelatinous sheath, containing 100 or more spores; spores globose to subglobose or subfusiform, 3.0–4.6 or 4.5–7.6 $\times$ 3.0–4.5μ. *Hymenium* I^+ wine-red. *Conidia* oval-fusiform, 3.1–3.7 $\times$ 1.8μ.

This species has been rarely collected in the southwestern United States, but it probably has a restricted Arid Southwestern distribution (Fig. 37) and will be found to be more abundant in Mexico. It grows on lightly shaded non-calcareous boulders, always in association with *P. euploca*.

TAXONOMIC REMARKS. This species probably involves a complex of several lower taxa. However, much more material must be collected over more of its range to be able to divide the group. This is probably a sorediate species, but soredia are not present on all parts of the thallus and sometimes may be rare or absent in any given collection; if abundant thallus is not collected. After close study, the holotype was found to be sorediate. Mexican material often has flat lobes. The epithecial reaction, spores and lobe shape do not appear to correlate yet with other characters to be able to divide the collections into discernable groups.

ARIZONA. COCHISE CO.: Chiricahua Mts., on trail to Silver Peak and Headquarters Gulch, NE of Southwestern Research Station, *Weber, Shushan & Anderson S-24630* (COLO), GRAHAM CO.: Coronado National Forest above Stockton Pass Campground, S of Safford, *Wetmore 14466 p.p.* (sub *P. euploca*). PIMA CO.: Tucson, Tumamoc Hill, *Blumer*, 1908 (DS, FH, MICH, W). Tucson Mts., *Darrow 1212* (THOMSON), *Darrow 1214* (COLO, THOMSON).

TEXAS. BREWSTER CO.: Big Bend National Park, across from Basin Campground, *Wetmore 14252A*; Boulder Meadows, *Wetmore 18491*; Grapevine Hills, NW of headquarters, *Wetmore 18293B*; Green Gulch, *Wetmore 18436, 18437A*.

Specimens also seen from Mexico.

Peltula polyspora (Tuck.) Wetm., comb. nov.

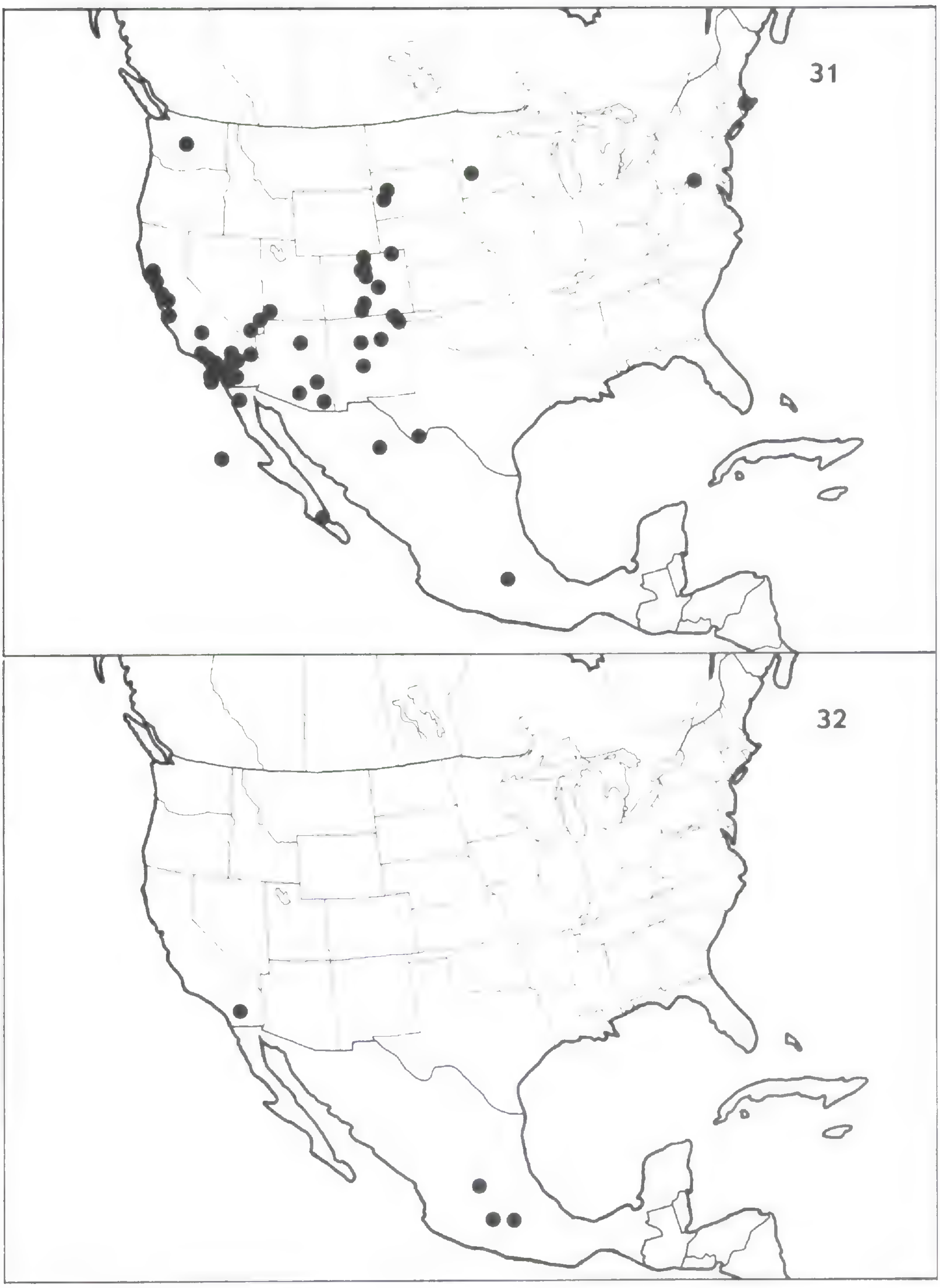
Heppia polyspora Tuck., Syn. N. Amer. Lich. 1: 115. 1882. *Endocarpiscum polysporum* (Tuck.) Fink, Contr. U. S. Natl. Herb. 14: 149. 1910. *Heppia arenivaga* Nyl., Lich. Jap. 104. 1890. TYPE: Colorado. *Brandegee*, 1879. (Holotype FH-TUCKERMAN; isotype US.)

Heppia terrena Nyl. *ex* Hasse, Bull. Torrey Bot. Cl. 24: 445. 1897. TYPE: California. Foothills of San Gabriel Mts., new Mt. Wilson's trail, 2500 ft., *Hasse FN 472*, 1896. (Lectotype NY; isolectotypes H-NYLANDER 30950, NY.)

Heppia leptopholis Nyl. *ex* Hasse, Lich. S. Calif. 10. 1898. TYPE: California. Santa Monica Foothills, on clay near Soldier's Home, *Hasse FN 526*. (Lectotype NY; isolectotypes H-NYLANDER 30944, N.Y.)

Heppia brouardii B. de Lesd., Bull. Soc. Bot. France 56: 475. 1909. TYPE: Mexico. "Peubla, Cerro Chiquihite, alt. 2205 m., sur la terre, *Frère Arsène Brouard*, 1906." No type material seen.)

NOMENCLATURAL REMARKS. Since no type was designated for *Heppia terrena*, I am selecting *Hasse Field Number 472* in NY as lectotype. The specimen in Nylander's herbarium was not selected because the original description was apparently not written by Nylander but by Hasse. The label data on some of the isotypes is incomplete.



FIGURES 31–32. The distribution of North American Heppiaceae.—31. *Peltula euploca*. —32. *P. michoacanensis*.

Heppia arenivaga Nyl was proposed as a *nomen novum* but was unncessary because no homonyms have been created.

I am selecting the specimen in NY as the lectotype of *Heppia leptopholis* for the same reason as in *H. terrena.* The label data varies on this collection—some with the same field number have the date 1896 and others 1897. These seem to be due to errors in copying labels. Some labels lack locality data.

No type material of *Heppia brouardii* was seen, and none may now exist. One collection identified as this species (*Arsène* 9633, US) agrees with the original description and was used in interpreting this species.

Thallus squamulose (Fig. 26), tan-olive, squamules 1–4 mm diameter, round to sometimes slightly lobed, flat; margins usually thickened and upturned; attached by tuft of hyphae in center. Squamules 183–336μ thick; upper cortex not developed; lower cortex of 2–3 layers of roundish cells, 30–40μ thick; medulla cellular; algal layer 61–122μ thick. *Apothecia* 1–20 per squamule, immersed; disc 0.2–1 mm diameter, occasionally with small thalloid rim; epithecium yellowish-brown, K^+ red-violet; hymenium 120–225μ thick; paraphyses 1.5–3.0μ thick; asci with gelatinous sheath (Fig. 7), 143–151 $\times$ 25–30μ, containing 100 or more spores; spores globose, 5.1–5.8 (–8.3)μ. *Hymenium* I^+ green becoming wine-red. *Conidia* fusiform, 3.7–4.3 $\times$ 1.2–2.8μ.

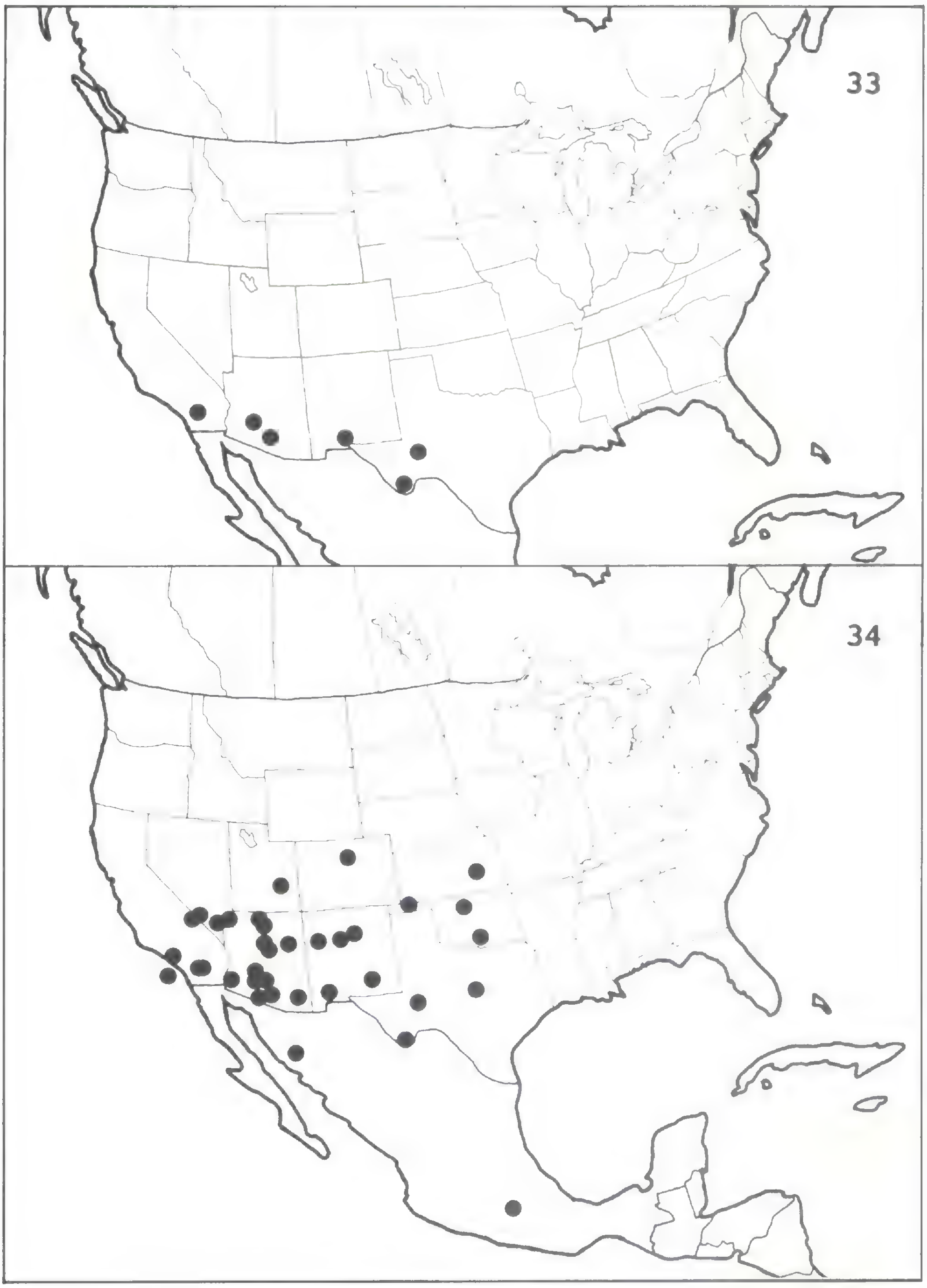
The distribution of *P. polyspora* in North America is somewhat uncertain, but it is probably basically an Arid Southwestern pattern (Fig. 38). The southern Rocky Mountain area needs further study. I found no *P. polyspora* when collecting in this area, but a few isolated plants may be found. This species grows in open dry areas on soil which is usually calcareous.

TAXONOMIC REMARKS. Collections with few apothecia have been called *Heppia terrena* and *H. leptopholis,* and those with many apothecia *H. polyspora.* But the production of apothecia is quite variable and does not correlate with any other character and is not worthy of taxonomic recognition.

Exsiccati: *Hasse, Lich. S. Calif. 680* (sub. *Heppia terrena*) (MINN, POM); *891* (sub *Heppia leptopholis*) (LAM, MINN, POM, WIS). *Plitt, Lich. Exs. 9* (sub *Heppia leptopholis*) (ABS, DS, FH, MU); *34* (sub *Heppia despreauxii*) (ABS); *239* (sub *Heppia terrena*) (DS, FH).

ARIZONA. COUNTY UNKNOWN: *Pringle 14* (FH, US). Santa Rita Mts., *Pringle 4* (COLO, FH, NY). MARICOPA CO.: Sauceda Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14543A.* PIMA CO.: Contano, *Darrow 527* (LAM). Organ Pipe Cactus National Monument below headquarters, *Sierk 2287* (SIERK). Tucson Mt. Park, *Imshaug 12890* (MSC). Ledges near Picture Rocks, 12 miles W of Tucson, *Bartram 736* (FH). Saguaro National Monument NW of Tucson, *Wetmore 14516C.* PINAL CO.: Picacho Pass NW of Tucson along Interstate 10, *Wetmore 14524, 14529B.* YUMA CO.: Near Mohawk, E of Yuma on US 80, *Wetmore 14544A, 14548B.*

CALIFORNIA. COUNTY UNKNOWN: Hall (MICH). KERN CO.: E of Maricopa on California 166, *Wetmore 14801, 14807.* LOS ANGELES CO.: San Gabriel Region, new Mt. Wilson trail, *Hasse FN 472* (H, NY). San Gabriel Range, *Hasse* [6 specimens collected between 1896 and 1904] (FH, MICH, MINN, NY, POM, US). San Gabriel Canyon, *Hasse,* 1892 (NY). Santa Monica Mts., *Hasse* [19 specimens collected between 1896 and 1908] (ABS, DS, FH, LAM, H, MICH, MINN, MU, POM, US, WIS); near Soldier's Home, *Hasse FN 526* (H, NY), 1897 (FH, MICH, NY, US). Verdigo Mts., *Hasse,* 1906 (FH). RIVERSIDE CO.: Cathedral City, *Rose 45338* (COLO); S of Cathedral City, *Wetmore 16862, 16867, 16871, 16875.* Near western edge of Palm Desert, *Wetmore 16834, 16835, 16849, 16854.* San Jacinto Mts., above Palm Desert, *Wetmore 14583A, 14601B.* Palm Springs,



FIGURES 33-34. The distribution of North American Heppiaceae.—33. *Peltula obscurans* var. *obscurans*.—34. *P. obscurans* var. *deserticola*.

Hasse "with *FN 829*" (FH), 1901 (NY), 1903 (FH, NY). San Jacinto Mts. at west edge of Palm Springs in Chino Canyon, *Wetmore 14612, 14621, 14622A, 14624A*. Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16876, 16893, 16898*. Eden Hot Springs, *Hasse*, 1911 (ABS). San Jacinto Mts. above Soboba Hot Springs (NE of Hemet), *Wetmore 14690, 14691, 14692A, 14693B, 14694, 14707, 14710, 14720*. SAN BERNARDINO CO.: E of South Pass, 12 miles W of Needles, *Drouet & McBride 4600* (F).

COLORADO. COUNTY UNKNOWN: *Brandegee*, 1879 (FH, US).

MINNESOTA. KANDIYOHI CO.: Locality unknown, *Looman*, 1961 (WIS). YELLOW MEDICINE CO.: Granite Falls, *Fink 498* (ABS, FH, MICH, MINN, MU, NY, US).

MONTANA. ROOSEVELT CO.: Locality unknown, *Looman*, 1961 (CANL, WIS).

NEBRASKA. CHERRY CO.: Valentine, in city park, *Wetmore 13098*.

NEVADA. NYE CO.: 41 miles ESE of Beaty, *Shushan Sl-4832* (COLO). CLARK CO.: Devils Canyon, S of Bunkerville on road to Lake Mead, *Tavares 1766* (UC). Along US 91 NE of Las Vegas 22 miles, on road to Axial, *Wetmore 17034, 17036, 17040, 17041*.

SOUTH DAKOTA. CUSTER CO.: Schenk Canyon (18 miles WSW of Custer), *Wetmore 11822* (MSC). GRANT CO.: Big Stone, *Williams*, 1894 (FH). PENNINGTON CO.: E of Hayward, 15 miles SW of Rapid City, *Wetmore 11046* (MSC, WETMORE).

TEXAS. BREWSTER CO.: Big Bend National Park, Green Gulch, *Wetmore 18443;* Old Mine Road near Rio Grande Village, *Wetmore 18378*. JOHNSON CO.: Cleburne State Park (SW of Cleburne), *Wetmore 14157*.

SASKATCHEWAN. ASSINIBOIA CO.: Locality unknown, *Looman*, 1961 (CANL). MIDALE CO.: Locality unknown, *Looman*, 1961 (WIS).

Specimens also seen from Mexico, Cuba, Canary Islands, and Italy.

Peltula richardsii (Herre) Wetm., comb. nov.

Heppia richardsii Herre, Bryologist 53: 297. 1950. TYPE: New Mexico. Sierra Co., Hot Springs, on dry sandy soil in crevices of rocks, 4000 ft., *Richards & Drouet 531*, 1939. (Holotype LAM; isotype F.)

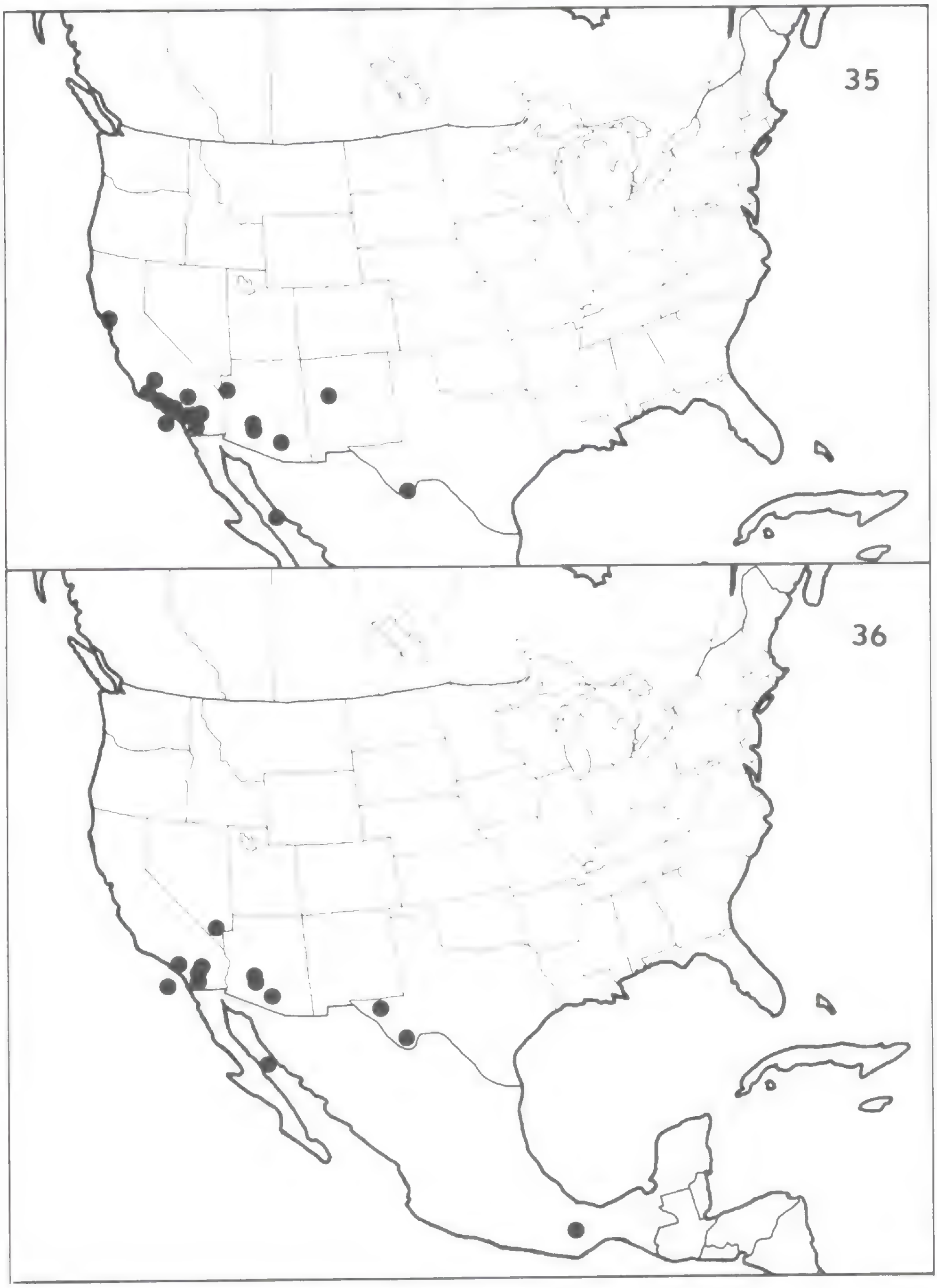
Thallus squamulose (Fig. 27), brown-olive; squamules 2–6(–10) mm diameter, round, concave or rarely convex; upper surface smooth and shiny; margin only slightly indented, downrolled; attached by tuft of large rhizines in center. Squamules 250–367μ thick; upper surface with amorphous layer over dead algal cells and cellular hyphae, 30–45μ thick; lower cortex not developed; medulla of loose hyphae; algal layer 75–105μ thick. *Apothecia* one per squamule (rarely 2–3), immersed; disc expanded, 0.5–3(–5) mm diameter, without thalloid rim; epithecium yellow-brown, K^+ red-violet; hymenium 165–170μ thick; paraphyses 1.5–3μ thick; asci with gelatinous sheath, 140–148 $\times$ 30–38μ, containing 100 or more spores; spores globose, 6.6–8.3μ. *Hymenium* I^+ wine-red. *Conidia* 3.1–3.7 $\times$ 1.2μ.

Prior to this study this species had been rarely collected, but in some areas I found it to be very abundant. It has an Arid Southwestern distribution (Fig. 39) and grows on soil, which is usually calcareous, in very dry habitats.

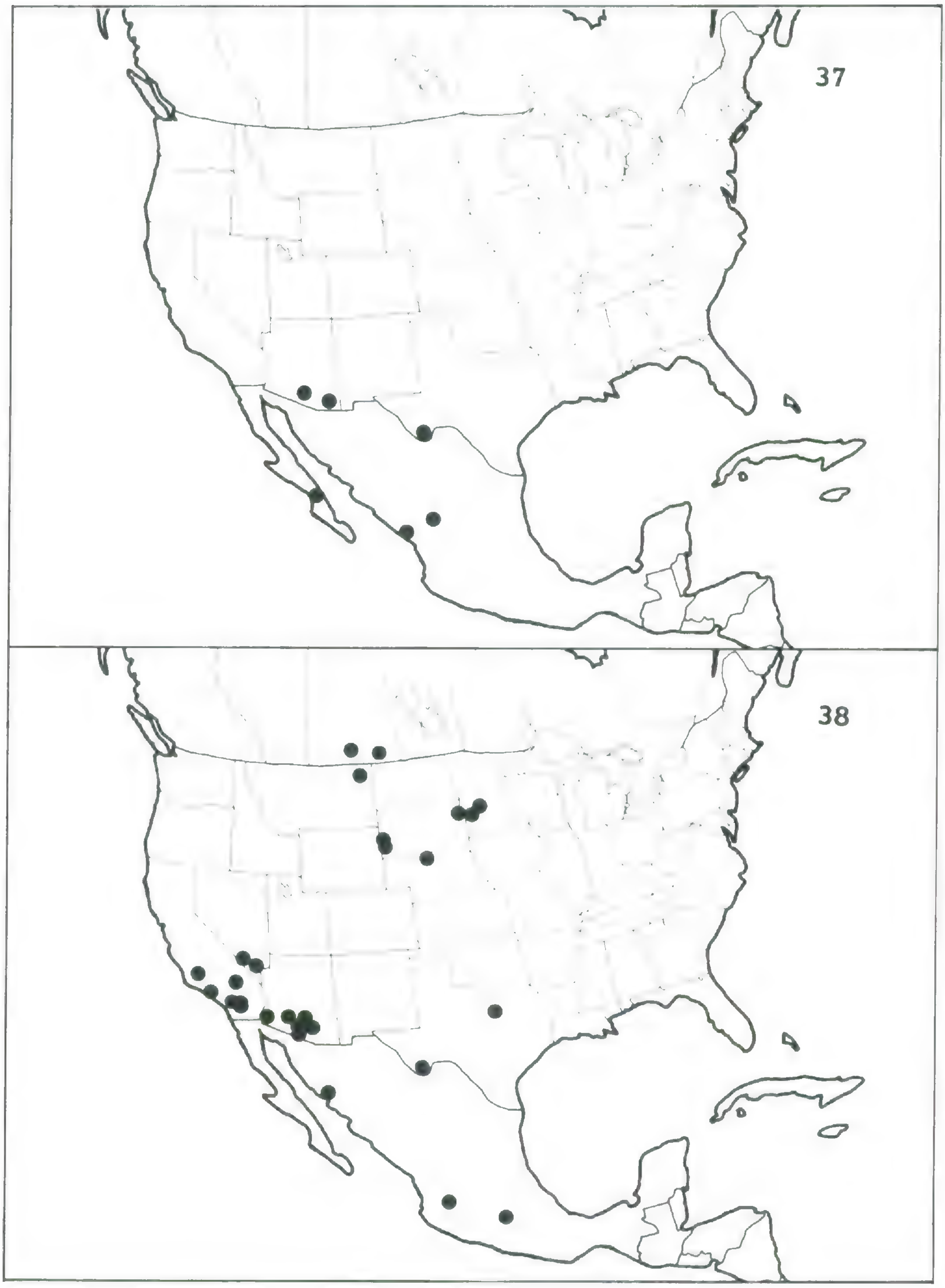
TAXONOMIC REMARKS. The large, shiny squamules with large apothecia easily separate this species from all others.

ARIZONA. MARICOPA CO.: Granite Reef, Forest Camp, *Sierk 2295* (SIFRK). N of Gila Bend near Buckeye on US 80, *Wetmore 14536*. Sauceda Mts., 14 miles S of Gila Bend, *Wetmore 14541*. PIMA CO.: Tucson, *collector unknown* [probably Blumer], 1908 (DS). PINAL CO.: Picacho Pass NW of Tucson along Interstate 10, *Wetmore 14529A*. YUMA CO.: Near Mohawk, E of Yuma on US 80, *Wetmore 14545*.

CALIFORNIA. RIVERSIDE CO.: San Jacinto Mts. at west edge of Palm Springs in Chino Canyon, *Wetmore 14615*. Near western edge of Palm Desert, *Wetmore 16846, 16858*. S of



FIGURES 35 36. The distribution of North American Heppiaceae.—35. *Peltula obscurans* var. *hassei*.—36. *P. omphaliza*.



FIGURES 37–38. The distribution of North American Heppiaceae.—37. *Peltula placodizans*.—38. *P. polyspora*.

Cathedral City, *Wetmore 16860.*

NEW MEXICO. SIERRA CO.: Hot Springs, *Richards & Drouet,* 1939 (F, LAM).

NEVADA. LINCOLN CO.: E of Meadow River between Rox and Carp, *Tavares 1261* (UC).

TEXAS. BREWSTER CO.: Big Bend National Park, W of junction going to Santa Elena Canyon along Texas 170, *Wetmore 14305;* 2 miles W of junction with road to Castolon, *Wetmore 18298;* Hot Springs near Rio Grande Village, *Wetmore 18185;* Old Mine Road near Rio Grande Village, *Wetmore 18380.*

Specimens also seen from Mexico.

Peltula tortuosa (Nees) Wetm., comb. nov.

Dufourea tortuosa Nees, Horae Phys. Berol. 43. *pl. 5, f.* 2. 1820. *Heterina tortuosa* (Nees) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 91. 1857. *Heppia tortuosa* (Nees) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 213. 1890 (= Étud. Lich. Brésil 1: 213. 1890). TYPE: Venezuela. Orinoco River, *Humboldt.* (Not seen.)

NOMENCLATURAL REMARKS. Nylander is often cited as the author of this species, but in his 1857 paper there is no description. Nees von Essenbeck indicates that he was describing a new species and did not refer to *Parmelia tortuosa* Ach., which is another species. See also comments by Henssen (1970).

Thallus subfruticose, olive-brown to olive-green; lobes flattened, upright, somewhat branched, often twisted and offset, occasionally partly terete, top often slightly flattened, surface smooth; nonsorediate, nonisidiate; attached by umbilicus. Thallus lobes 3–7 mm long, 0.1–0.2 mm thick, 0.4–1.0 mm wide; corticate all around, cortex of 3–4 layers of cells, 10–18μ thick; medulla of loose hyphae with hollow areas; algal layer all around, 40–80μ thick. *Apothecia* produced on the sides or in swollen ends of lobes, several per lobe, totally immersed with punctiform disc or disc slightly enlarging with age; epithecium yellowish-brown, K^-; hymenium 150–250μ thick; paraphyses thin (1.0–1.5μ), branched but capitate; asci with gelatinous sheath, containing 100 or more spores, 18–25 $\times$ 83–110μ; spores globose or subglobose, 4.5 $\times$ 3.0–4.5μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 3.1–3.7 $\times$ 1.2μ.

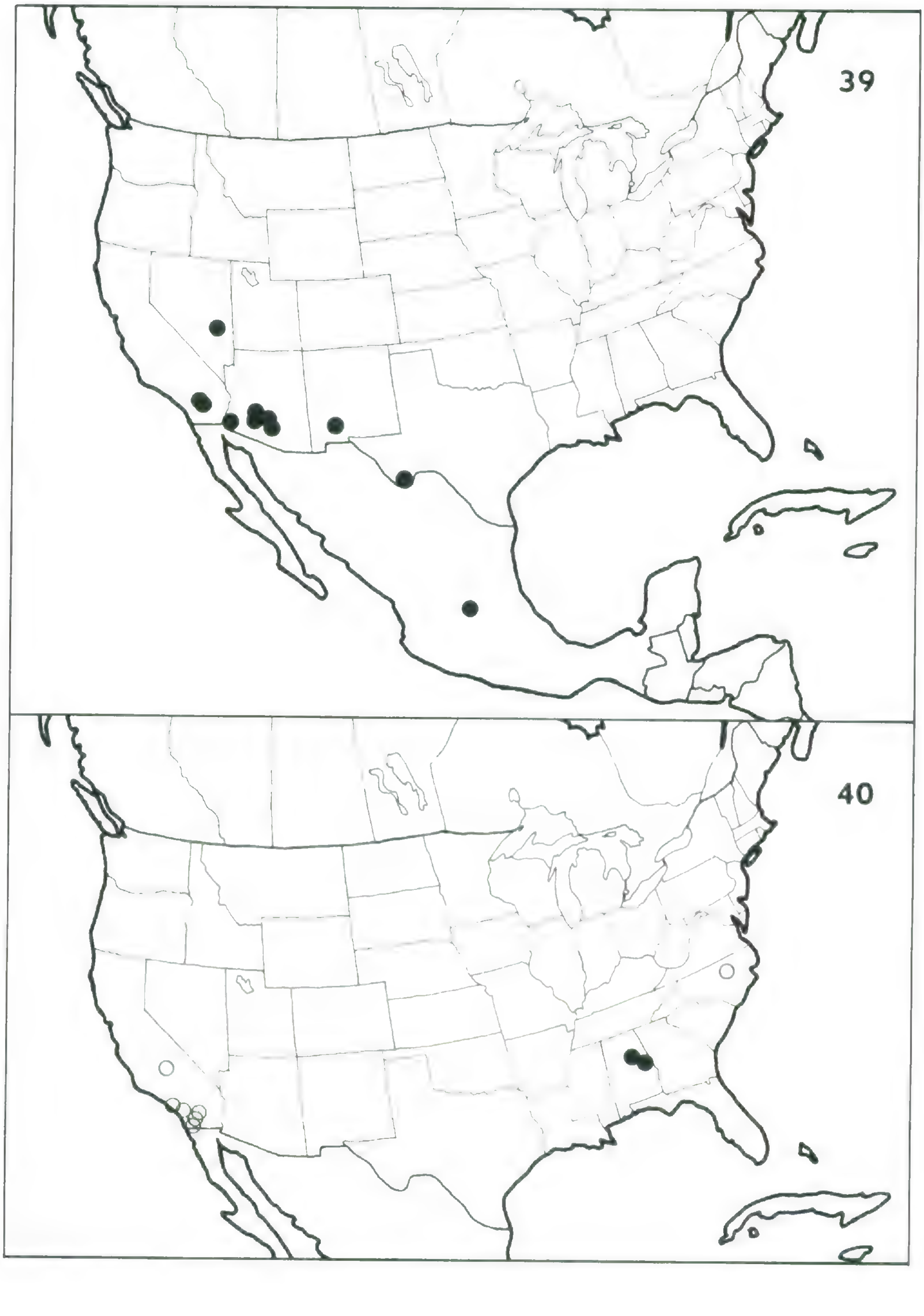
This species has an uncertain distribution type (Fig. 40) in North America, since I have only seen two collections, both sent to me by Aino Henssen, within the area of this study. It probably will be found in more localities in the future. It grows on granitic rocks. Previous records from Chiricahua Mts., Arizona by Weber (1963) are erroneous. The specimens are *P. clavata.* Henssen (1970) includes some specimens of *P. cylindrica* with *P. tortuosa* in her paper.

ALABAMA. RANDOLPH CO.: 6 km W of Wadley, E of Ashland, *Henssen 17181B* (HENSSEN, WETMORE). ST. CLAIR CO.: Cook Springs, 13 km E of Leeds along US 78, *Henssen 15187A* (HENSSEN, WETMORE).

Specimens also seen from Africa and Venezuela.

Peltula zahlbruckneri (Hasse) Wetm., comb. nov.

Heppia zahlbruckneri Hasse, Bryologist 14: 100. 1911. TYPE: California. Rubio Canyon, San Gabriel Gelage bei Pasadena, 2500 ft., *Kingman 1159,* 1911. (Holotype W; isotype FH.)



FIGURES 39 40. The distribution of North American Heppiaceae.—39. *Peltula richardsii*.—40. *P. tortuosa*, closed circle; *P. zahlbruckneri*, open circle.

NOMENCLATURAL REMARKS. The *Krypt. Vind. Exs. 1965* indicates that the collection is the "original" collection, however, it also gives Hasse as the collector instead of Kingman so it cannot be the type collection.

Thallus areolate-squamulose or sometimes minutely subfruticose (Fig. 28), tan to brownish-olive; squamules swollen, lobed at margins, convex, tops often flattened (especially when young), 0.5–2 mm wide; attached by short stalk and umbilicus. Squamules 153–306μ thick; upper cortex not developed; lower cortex with 3–6 layers of roundish cells, 30–56μ thick; medulla of loose hyphae with hollow areas; algal layer 75–150μ thick. *Apothecia* 1–7 per areole, totally immersed; disc punctiform, without thalloid rim; epithecium brownish, K ; hymenium 105–150μ thick; paraphyses 1.5–3μ thick; asci with gelatinous sheath, 98–113 $\times$ 18–23μ, containing 32–100 or more spores; spores globose to subglobose, 4.5–7.6 $\times$ 3.0–4.5μ. *Hymenium* I^+ wine-red. *Conidia* fusiform, 3.0–4.5 $\times$ 1.5μ.

P. zahlbruckneri occurs in southern California and North Carolina according to present information (Fig. 40), but it probably will be found in other places also. It grows on the north sides of large granite rock ledges and covers large areas in some localities (*e.g.*, Palm Springs, California, Fig. 15).

When I visited Rubio Canyon (the type locality) in 1966, no undisturbed rock areas could be found, and a large housing development had been built in the canyon.

TAXONOMIC REMARKS. Young asci have over 100 spores, but as the ascus matures fewer spores are found. In some cases I have seen about 60. Hasse mentioned 24–32 in the original description, but some apothecia of the type have 100 spores. This species never gets tall and cylindrical like *P. cylindricia,* but in some other ways these two species are similar.

Exsiccati: *Krypt. Vind. Exsicc. 1965* (F, FH, NY, US). *Plitt, Lich. Exs. 60* (ABS, FH, OS, MU).

CALIFORNIA. LOS ANGELES CO.: San Gabriel Range, *Hasse* (MICH); Pasadena, *Kingman 1159* (FH, W), *1310* (ABS); Rubio Canyon, *Hasse,* 1911 (ABS, FH), *Hasse,* 1911 (ABS, LAM), *Hasse,* 15 April 1911 (FH, US), *Hasse* (F, FH, NY, US), *collector unknown,* May 1911 (FH). Santa Monica Range, *Hasse,* 1913 (ABS, FH, OC, OS); Topanga Canyon, *collector unknown,* 1901 (FH). RIVERSIDE CO.: Eden Hot Springs, *Hasse,* 1911 (FH, US). San Jacinto Mts., above Palm Desert, *Wetmore 14582, 14591;* near western edge of Palm Desert, *Wetmore 16857.* Palm Springs, *Hasse,* 1903 (FH, NY, US); west edge of Palm Springs in Chino Canyon, *Wetmore 14608.* Palm Canyon S of California 111, *Wetmore 16881B, 16897A.* Near Riverside, *Reed 3171* (FH). SAN DIEGO CO.: One mile NW of Descanso, *Wetmore 16972.* TULARE CO.: 3 miles SE of Exeter at Rocky Hill, *Weber L-38587* (COLO). VENTURA CO.: 4 miles N of Newbury Park on Ventura Blvd., *Weber S-1748* (COLO).

NORTH CAROLINA. WAKE CO.: 30 km N of Raleigh, south bank of Little River, *Henssen 17162B* (WETMORE).

SPECIES OF DOUBTFUL PLACEMENT AND ERRONEOUS RECORDS

Heppia alumenensis Herre, Broyologist 15: 84. 1912.—The type collection could not be found in any North American herbarium, nor was it in Vienna. No authentic material has been found, and no material has been seen that has ever been given this name. Collections made at the type locality (Alum Rock Park, California) by Tavares and her students failed to turn up any Heppiaceae that agreed with the original description. The type may have

been destroyed, or it may yet turn up in some herbarium. Placement of this taxon must await finding authentic material.

Heppia planescens Nyl., Syn. Lich. 2: 46. 1885.—The type could not be located in Helsinki. It was apparently sent to Hariot in Paris on loan in 1914 and never returned. It may someday be found in Paris. No other authentic material has been seen, and none is in the Tuckerman Herbarium (FH).

Heppia psammophila Nyl., Flora 61: 339. 1878. Hasse (1915) reported this species from Barton's Peak, Santa Monica Range, California, but no specimen from that locality has been seen. No other records of *H. psammophila* were found and the report is probably based on an incorrect identification. I have examined the type in Nylander's herbarium (H), and I have seen no North American material that can be assigned to this species.

Index to Exsiccati

In this list only collections from North America are included.

Hasse, Lich. S. Calif. 680 (sub *Heppia terrena*) = *Peltula polyspora* (MINN, POM).
Hasse, Lich. S. Calif. 891 (sub *Heppia leptopholis*) = *Peltula polyspora* (LAM, MINN, POM, WIS).
Krypt. Vind. Exs. 1965 (sub *Heppia zahlbruckneri*) = *Peltula zahlbruckneri* (ABS, FH, OS, MU).
Plitt, Lich. Exs. 9 (sub *Heppia leptopholis*) = *Peltula polyspora* (ABS, DS, FH, MU).
Plitt, Lich. Exs. 34 (sub *Heppia despreauxii*) = *Heppia lutosa* (DS, FH, MU); = *Peltula* polyspora (ABS).
Plitt, Lich. Exs. 35 (sub *Heppia hassei*) = *Peltula obscurans* var. *hassei* (FH); = *Peltula obscurans* var. *obscurans* (ABS, FH).
Plitt, Lich. Exs. 138 (sub *Heppia bolanderi*) = *Peltula bolanderi* (ABS, FH, MU); = *Pelutla obscurans* var. *deserticola* (DS).
Plitt, Lich. Exs. 139 (sub *Heppia polyspora*) = *Peltula bolanderi* (ABS. FH); = *Peltula obscurans* var. *hassei* (DS, MU).
Plitt, Lich. Exs. 238 (sub *Heppia conchiloba*) = *Peltula obscurans* var. *hassei* (ABS, F, FH, MU).
Plitt, Lich. Exs. 239 (sub *Heppia terrena*) = *Peltula polyspora* (DS, FH); = *Heppia lutosa* (ABS, MU).
Zahlbr., Lich. Rar. 90 (sub *Heppia bolanderi*) = *Peltula bolanderi* (FH).

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PHYTOGEOGRAPHY AND TAXONOMY OF *PINUS* SUBSECTION *BALFOURIANAE*[1]

D. K. Bailey[2]

Abstract

The populations comprising the foxtail-bristlecone pine complex (*Pinus* sect. *Parrya* Mayr. subsect. *Balfourianae* Engelm.) are shown to be separable into three allopatric forms each with easily observed distinguishing characters. To recognize, as is done at present, only two species (*Pinus aristata* Engelm. and *Pinus balfouriana* Grev. & Balf.) is clearly unsatisfactory, and a third species, *Pinus longaeva*, is described to represent the population hitherto considered to be *Pinus aristata* Engelm. but lying to the west of the Colorado-Green River system in Utah, Nevada, and California. *Pinus aristata, sensu stricto*, is thus confined to Colorado, New Mexico, and Arizona.

Historical Introduction

Foxtail pines, *Pinus balfouriana* Grev. & Balf., and bristlecone pines, *Pinus aristata* Engelm. (sect. *Parrya* Mayr subsect. *Balfourianae* Engelm.), are closely related Tertiary relics confined to high elevations in certain mountainous areas of six contiguous southwestern states—Colorado, New Mexico, Arizona, Utah, Nevada, and California. With the possible exception of the recently described *Pinus rzedowskii* Madrigal & Caballero from Michoacán, Mexico (Madrigal & Caballero, 1969), they have no close relatives elsewhere, although they exhibit certain interesting affinities with the pinyon pines (sect. *Parrya* Mayr subsect. *Cembroides* Engelm.). Probably because of their natural inaccessibility, the foxtail and bristlecone pines seem to have received less critical attention than many other pines of western North America.

The foxtail pine was the first to be described (Greville & Balfour *in* Murray, 1853) on the basis of specimens collected for the Scottish Oregon Association by Jeffrey in 1852 on Scott Mountain in the Klamath Mountains of northern California. The type specimen is in the herbarium of the Royal Botanic Garden at Edinburgh.

Based on material collected in Colorado by C. C. Parry in 1861[3] from the regions of Pikes Peak and the headwaters of Clear Creek, Engelmann (1863)

[1]The author acknowledges with thanks the support of the Isotope Foundation of Los Angeles for most of the field work beyond the State of Colorado and expenses for publication. The author also thanks his own organization for permitting him to conduct the work of this study in part on official time and for technical services. A detailed acknowledgment of the assistance received by the author from individuals, universities, government and private organizations appears at the end.

[2]Environmental Research Laboratories, National Oceanic and Atmospheric Administration, Boulder, Colorado 80302.

[3]The oldest herbarium specimens of *P. aristata* from Colorado are three branch specimens without cones collected in the course of Frémont's second expedition to California, 1843–1844. The provenance and date of collection are not given, but from Frémont's known route it may be deduced that the specimens were collected from the vicinity of South Park and possibly from Kenosha Pass in June, 1844. Two of these specimens are preserved in US and the third in GH. There are also two specimens without cones collected in the course of Gunnison's Pacific Railroad survey in the summer of 1853 from Cochetopa Pass. One of these is in NY and the other in GH. The latter collection was known to Engelmann (1863).

described the bristlecone pine. Owing to an unforeseen delay in printing, the full description (Engelmann, 1863) of *Pinus aristata* did not appear until after an abridged account (Parry & Engelmann, 1862). This delay explains the reference, in the abridged account, to the full description as if it were already published. Engelmann's type specimen is in the herbarium of the Missouri Botanical Garden at St. Louis.

Because of the obscure manner of publication it seems unlikely that Engelmann became aware of *Pinus balfouriana* until some years after he published the description of *P. aristata.* In any case the description of *P. balfouriana* was misleading because the fascicle illustration showed only four needles and the account stated that fascicles were variable in needle content from 2 to 5. Thus the impression was created that most fascicles probably contained less than what is in fact the usual 5 needles. Examination of the type specimen shows, according to H. R. Fletcher (personal communication, 1970), that Jeffrey collected a branch containing many fascicles of 4 needles. The confusion created by the original description persisted at least through the publication of the second edition of Gordon's *Pinetum* (Gordon, 1875). Gordon described *P. balfouriana* as having "leaves mostly in fours" and gave *Pinus quadrifolia* Parry from near San Diego as a synonym.

In 1868, in the course of the 40th Parallel Survey, Sereno Watson (1871) collected pine specimens from the southern extension of the East Humboldt Mountains (now known as the Ruby Range) of Nevada, which he determined as "*Pinus balfouriana* Murr." The closing of his description states that "the Colorado form, (*P. aristata,* Eng., which has been identified with this species by Dr. Engelmann,) has smaller cones, 2–3′ long[4], dark-colored, the lance-subulate awn often 3″ long[5]." Thus Engelmann must have encountered *P. balfouriana* some time before 1871 and was already thinking of *P. aristata* as a form of *P. balfouriana.* In this connection a specimen should be noted in the herbarium of the Missouri Botanical Garden (MO 2001034) collected by William Gabb from the "eastern declivity of the White Mountains" of California in July, 1867. It is labelled *P. aristata* var. *decurva* in a hand that appears to be Engelmann's. It is not known when the label was written nor what was intended by the unpublished *"decurva,"* but the writer could possibly have been recognizing a branching habit described by Watson (1871) as "pendulous or spreading . . . often short and twisted." This branch characteristic, as shown very slightly in Fig. 1 and in well-developed form in Fig. 2, is common among the bristlecone pines from the Great Basin but is nearly absent from the Colorado trees. Gabb's specimen was originally deposited in the George Engelmann Herbarium and seems to be the earliest from the regions west of Colorado. The earliest bristlecone pine specimen from Arizona was probably collected in 1871 by Bischoff with Lt. Wheeler's Expedition; it is now preserved at St. Louis (MO 1838454).

Some years later, in his revision of the genus *Pinus,* Engelmann (1880) compressed the foxtail-bristlecone pine complex into a single species, which on

[4]The notation 2–3′ means 2 3 inches long.
[5]The notation 3″ long means 3 lines long. A line is 1/12 of an inch.

Figures 1–2.—Tree forms.—1. Tree of Population I, elevation 3500 m, showing characteristic erect, somewhat fastigiate branching. Thompson Gulch, Silver Plume Mountain, Colorado (Clear Creek County)—2. Tree of Population II, elevation 3400 m, showing characteristic pendulous and twisted branching. Mt. Washington, Nevada (White Pine County). Photograph courtesy of A. H. Holmgren.

the basis of priority was called *P. balfouriana.* His explanatory note reads as follows: "*P. balfouriana,* Jeffrey, and *P. aristata,* Engelm., of the Colorado Rocky Mountains, are identical in leaf structure and in flowers and must be united, though the cone of the former is elongated, often even cylindrical, the apophyses thicker and peculiarly spongy, and at maturity unarmed, while the other has an oval cone with thinner scales and awnlike prickles. In Utah and Nevada a form occurs with cones like the latter, but with short, stout, recurved prickles." These remarks regarding the Utah and Nevada forms are remarkably accurate in most respects as will be shown below, but in asserting identical leaf structure Engelmann was correct only when comparing *P. balfouriana* with bristlecone specimens from Utah, Nevada, or California. Evidently Engelmann did not compare the leaf structure of *P. balfouriana* with a Colorado bristlecone pine. The latter he showed very clearly and correctly (Engelmann, 1863: Pl. 6, Figs. 4–8). The needle cross sections shown in Figs. 6–8 are in fact far more accurate in subtle but important details than is the much later cross section given by Shaw (1914). Engelmann (1880) created a taxon one rank above species but well below the rank of genus to include the foxtail-bristlecone complex. He called the taxon *Balfouriana* and gave it in the singular form, possibly because he believed it to contain but a single species. This taxon was conserved as a "Group" by Shaw (1914) who stated it in the plural form, *Balfourianae.* In a recent revision of the genus *Pinus* by Critchfield and Little (1966) the taxon

is designated subsection *Balfourianae* Shaw. The oversight in attributing the epithet to Shaw is corrected later in Little and Critchfield (1969), where it is given as subsection *Balfourianae* Engelm.

Engelmann persisted in his attempts to demote his species, *Pinus aristata,* and in the section on Coniferae which he contributed to the *Botany of California* (Watson, 1880), he indicated it as *P. Balfouriana* Jeffrey var. *aristata* Engelm. Engelmann's demotion of *P. aristata* has not been accepted by later botanists, who have continued in manuals and monographs down to the present to consider that subsection *Balfourianae* consists of two species, *P. balfouriana* and *P. aristata* (*cf.* Critchfield & Little, 1966). One of the purposes of the present account is to get to the root of the confusion in what is currently termed *P. aristata* and to show that Engelmann's species *P. aristata* is indeed a good species.

Background of the Present Study

This investigation is the direct outcome of a long-standing interest in phytogeography and in dendrochronology with particular reference to their geophysical and climatological implications. At first much weekend and otherwise free time was spent exploring the Colorado mountains seeking stands of bristlecone pine, in the hope of finding stands containing trees old enough to be of interest for dendrochronological studies. After some five years of searching without finding any unusually long-lived specimens the decision was taken to move farther afield and examine the much longer-lived bristlecone pines of Nevada and the White Mountains of California. Accordingly in late August, 1968, the search was extended, in company with personnel of the University of Arizona, to the bristlecone pines in the Snake Range of eastern Nevada and the newly found stand on Pearl Peak in the Ruby Range of Elko County, Nevada. The first encounter with specimens in the Wheeler Peak Scenic Area revealed on obvious difference between the Nevada and the Colorado trees. The foliage was not liberally dotted with the white crusty resin exudations or dots which, without exception, characterize the Colorado trees. On this and several later trips to inspect additional stands of bristlecone pine in Utah, Nevada, and California, it became increasingly evident that practically all the trees lacked the conspicuous resin exudations, termed "dandruff," for short, of the Colorado trees.

An additional discovery soon followed, however, that has proved of even greater value. As stated earlier Engelmann represented the needle morphology of *Pinus aristata* with remarkable precision (Engelmann, 1863: Pl. 6). Colorado trees possess needles with single resin ducts in the distal quarter in three-fourths or more of all needles examined. About one-half of the needles had single resin ducts for their entire length, and only about one-fourth of the needles showed two ducts for their entire length. These properties vary from specimen to specimen and perhaps from locality to locality in ways that will be discussed further below. Besides having no obvious "dandruff," the bristlecone pines from Nevada almost invariably have two resin ducts for the entire needle length. Since resin ducts in subsection *Balfourianae* are always external (*cf.* Shaw, 1914) and the lines of stomata confined to ventral surfaces of the needles, the resin ducts are easily

seen with a hand lens as the dark lines along the dorsal needle surface. Often they can be seen without optical assistance.

It was these discoveries that led to the studies now reported.

GEOGRAPHIC DISTRIBUTION OF THE DISTINCT POPULATIONS OF SUBSECTION BALFOURIANAE

Almost from the first it became evident that the characteristics and distribution of *Pinus balfouriana,* the foxtail pine, would have to be considered in addition to those of the bristlecones. Fresh branch specimens collected for this study by the U. S. Forest Service showed, on the basis of external features of foliage, that the foxtails could not be distinguished from the bristlecones from Nevada and California. The taxonomic distinction rests mainly on the cones.

In view of the taxonomic problems that clearly exist it was decided, at first, to avoid specific names by describing the verifiable stands of trees according to their characteristics by population number as follows:

Population	Determining Characteristics
I	Numerous resin exudations on needles and a high frequency of single resin ducts along the entire or the distal portions of the needles; cones with stout bristles, especially at the often flattened base.
II	Almost no resin exudations on needles and with practically all needles having two resin ducts; cones with fine bristles, often reduced or missing at the usually rounded base.
III	Foliage identical in external features with Population II, but found in the southern Sierra Nevada; cones with conical bases and fewer scales than cones in Populations I and II, and with minute bristles.
IV	Almost identical with Population III but found in the Klamath Mountains of northern California; with somewhat broader cone scales than found in Population III.

Separation into Populations I and II, both up to the present time regarded as *Pinus aristata,* can thus be made solely on the basis of foliage as long as specimens come from localities to the east of the Sierra Nevada. The foliage may be either dried, as found in herbaria, or fresh. Separation into Populations III and IV, the disjunct populations of *P. balfouriana,* is usually made according to collection locality.

Critchfield and Little (1966) published distribution maps for *Pinus aristata* and *P. balfouriana.* Their data for *P. balfouriana* proved entirely satisfactory. Nevertheless new maps based on actual examination of herbarium and fresh material, were made in this study. The Critchfield and Little map of the distribution of *P. aristata* could not be used because it took no account of the characteristics indicated above, and it was necessary therefore to compile an entirely new map. To accomplish this some 17 herbaria were visited, and four

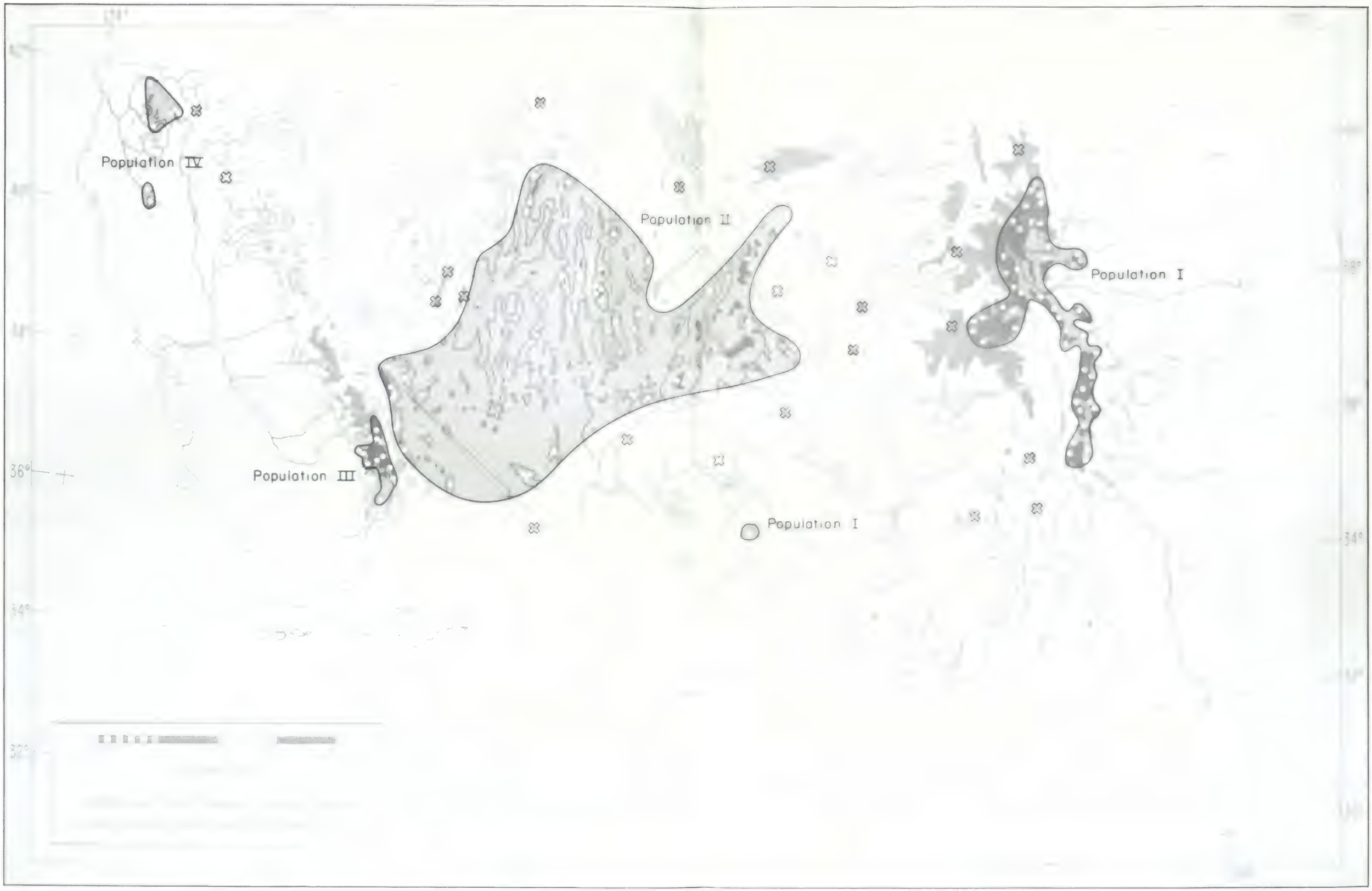

Figure 3.—Geographical distribution, illustrated by selected stations, of the four populations of *Pinus* subsect. *Balfourianae* Engelm. Open ×'s indicate locations with suitable habitats, where the pines, though recently looked for, have not been found.

additional ones were consulted. Several field trips were made to verify stands and establish the population to which each belonged. Some collecting of fresh material was also done by the author and for him not only by the U. S. Forest Service, but also by the Museum of Northern Arizona, the Laboratory of Tree-Ring Research, and by R. J. Mastrogiuseppe. The results of this survey are indicated in Appendix I in order of number of specimens of subsect. *Balfourianae* available. In all more than 600 specimens were examined. Each specimen that could be personally examined was assigned a population number and card-indexed for collector, date, locality, site information, and any particularly noteworthy characters. Cones, when available, were also examined and any peculiarities noted. For the herbaria not personally visited, the specimens were assigned population numbers based on the experience gained from the specimens that could be examined. Two comments should be made concerning the herbarium specimens actually examined. First, without more care than is usually given, the cones lose some or nearly all their bristles. Second, some specimens of Population I fail to show the resin exudations in a normal way. Instead they have a varnished appearance that is almost certainly due to heating before or during their herbarium preparation. Fresh branch specimens left in a sun-heated car became similarly altered in appearance. There were also many specimens, particularly older ones, for which the collection locality was stated too generally for them to be used in making the distribution map.

The results of the survey were collected by localities and reduced to a series of specific locations.[6] In most cases the coordinates of the plotted points are known to within 2 km. Often a plotted location represents as many as five or ten specimens. When separate localities were too close for convenient plotting, all but one were omitted since the purpose of the map, shown as Fig. 3, was to indicate only general distribution, with particular attention to limits of range. Because of the highly localized nature of the stands at high elevations, it seemed unwise to indicate any sort of continuous distribution. It should be pointed out that the plotted points represent anywhere from a single tree (in the Last Chance Mountains of California) to extensive open forest stands (for example the Ancient Bristlecone Pine Area, White Mountains of California and the Mt. Evans stands in Colorado). To indicate the high-altitude habitats of the trees, the distribution map shows 2000 and 3000 m contours. Specimens from Populations I and II are found up to timberline at maximum elevations between 3500 and 3700 m. Trees of Population I reach lower limits at about 2500 m, but trees of Population II have been found at elevations as low as 2200 m. Population III trees have upper limits similar to Population I. Mastrogiuseppe (personal communication, 1970) has recently found a stand of Population III trees at about 2300 m, an elevation that must be very close to its lower limit. Trees of Population IV occur the farthest north, in mountains lower than those which harbor trees of the first three populations. Elevation limits for trees of Population IV seem to be between about 1950 and 2750 m.

[6]Details of the survey of herbaria, and the reduction of the data are deposited at the Herbarium of the University of Colorado (COLO).

The geographical distributions of Fig. 3 exhibit nothing new about Populations III and IV, but the map reveals a complete separation of Populations I and II. Particular note should be taken of the highly disjunct stands of Population I trees in the San Francisco Peaks of northern Arizona. The low, hot, and very dry lands along the Colorado-Green River system seem to mark the excluded territory for both populations. A rough boundary line has been drawn around the dots representing each population. While stands, in addition to those deliberately omitted for plotting convenience, will almost certainly be found within the boundary lines, it will be of considerably greater interest to see whether further searches will locate stands outside the boundaries shown. In the latter connection, mountainous regions having suitable habitats in which recent searches have failed to find bristlecone or foxtail pines (without regard to unsupported earlier claims as to their presence in some cases) are indicated by open ×'s on the map. Thus some of the ×'s represent stands of limber pine, *Pinus flexilis* James, that were mistakenly reported as bristlecone pine.

Only one locality shown in the Population II area has not been verified, as far as could be learned, with a specimen. It is the point at the southern end of the Monitor Range of Nevada, which was taken from an updated manuscript map provided by E. L. Little, Jr. (personal communication, 1970). Acceptance of this stand places the Population II boundary along the Monitor Valley in central Nevada. The most northeasterly location shown within the Population II boundary is an approximate position in Sowers Canyon, Utah. It is based on information supplied by R. M. Lanner (personal communication, 1970). This location seems to be supported by a somewhat vaguely described collection made by Marcus Jones in 1908. Also, the locality shown for Population I trees in the Wet Mountains of Colorado does not seem to be supported by any herbarium specimens.

In concluding this stage of the discussion of the geographic distribution it should be stated that no significant examples of intermediate form or intergrading could be found between Populations I and II. However, the Arizona trees seem to exhibit somewhat fewer resin exudations than trees from Colorado and New Mexico. Moreover a single tree within the Population II region, out of the many hundreds of Population II trees and herbarium specimens examined, showed perceptible resin exudations, comparable with specimens with the fewest resin exudations of Population I from Arizona. This specimen possessed two resin ducts per needle in the normal way and had typical Population II cones. It was found among quite normal trees in Bryce Canyon National Park of southern Utah. A few herbarium specimens from southern Utah have also shown more than the typical frequency of resin exudations, but in all cases far below that typical of Population I. The matter of intermediate or intergrading forms between Populations II and III is less clear cut. In examining herbarium cone specimens a few were found from the Population II area which had somewhat fleshly apophyses, somewhat fewer than normal cone scales, and that were almost without the typical bristles. Cones of this type, resembling Population III cones, have been found not only in the White (Mirov, 1967) and Inyo Mountains, just across the

Owens Valley from the Population III stands, but also from as far east as Morey Peak in the Hot Creek Range of central Nevada. Most trees in these areas are, however, good representatives of Population II, and the rarities, reported above, are too exceptional if not freakish to be considered in further detail at this stage of study.

Details of Distinguishing Characters

With the recognition and mapping of the distinct populations of the foxtail-bristlecone pine complex, it is now necessary to investigate in greater detail not only the distinguishing characters already used to sort the populations but also additional characters.

FOLIAGE—EXTERNALLY OBSERVABLE FEATURES

All pines of the foxtail-bristlecone complex have five needles in an overwhelmingly large fraction of the fascicles. Fascicles of four occasionally occur, as has been mentioned earlier, but they are rare. In the several thousand fascicles examined in the course of this study only a few dozen possessed less than four or more than five needles. However, fascicles of two needles and of up to eight needles have been found. In the detailed studies that follow only fascicles of five have been used. This deliberate selection can have had no measurable effect on the findings.

Two easily determined properties of the needles have been studied statistically, using discrete samples of 20 fascicles (100 needles) from each branch specimen. First, the number of needles per fascicle with one or more resin exudations (see Fig. 4) on the dorsal surface was determined. The resin exudations form during the first-year needle elongation and persist with little further change throughout the life of the needle. Second, with the same samples and at the same time the number of needles per fascicle having single resin ducts was determined.

It was apparent from the first that trees of Population I often had needles with more than one resin exudation. Moreover, under a hand lens the resin exudations exhibited a crusty, crazed surface that scattered light well and made them whitish and conspicuous. Resin exudations on needles from Populations II, III, and IV were rare, and cases of more than one exudation per needle were exceedingly rare. In most cases the exudations were transparent and comparatively smooth surfaced. This property made them so inconspicuous that a hand lens or close examination was usually required to find them. Care was taken to avoid needles which showed evidence of having had resin physically transferred to them, for example, from a nearby cone or from an injury. These differences in appearance of the resin exudations are probably a direct consequence of differences in the physical and chemical properties of the needle resins. It should be recognized that by not counting more than one resin exudation per needle, some of the inherent variability in the "dandruffy" appearance of trees of Population I is not measured.

In determining and recording the number of needles with single resin ducts an arbitrary procedure was adopted in order to avoid tedious complications of

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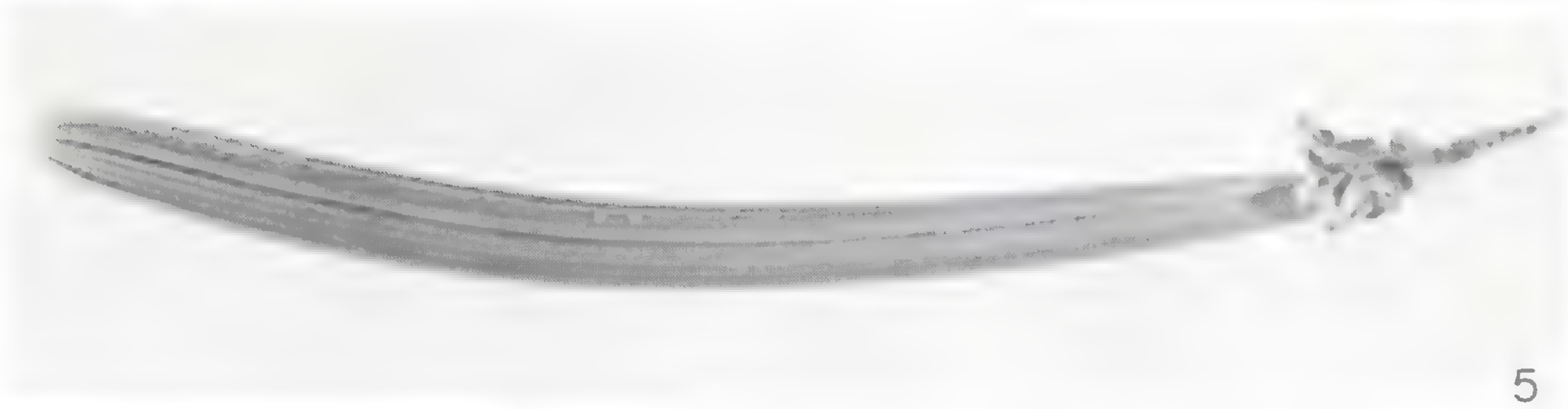

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doubtful significance. It affects mainly trees of Population I, and obscures some of the inherent variability in the number of resin ducts. Needes were counted as having a single resin duct if the distal quarter, approximately, had a single duct without regard to the occurrence of one, two, and very rarely three ducts along all or part of the remaining three-quarters of the needle. It was observed that needles having single ducts proximally, but terminating with two ducts, were almost non-existent. Any needle terminating in two ducts always had two and sometimes three ducts (for short intervals) along the rest of its length. The resin ducts in trees of Population I are placed below a shallow longitudinal groove in the dorsal surface. It is the groove that is easily seen and counted as a duct. Populations II, III, and IV do not possess such grooves, but their large resin ducts are plainly visible as a pair of parallel dark lines along the dorsal surface of the needles. In these populations the number of ducts along a particular needle seems to be almost invariable. A few needles have single ducts, but the great majority have two. Examples with three ducts are exceedingly rare, and only a single very thin needle was encountered that appeared to have no resin duct. In needles with two ducts, the spacing of the ducts is variable, often far apart in Populations II, III, and IV, and close together in Population I. These diagnostic characters are illustrated in the fascicle photographs in Figs. 4–7.

Figure 8 contains the results of the studies as histograms each representing 200 fascicles grouped to show the difference between Population I trees from the Rocky Mountains and from Arizona, and the similarity of Population II trees with those of Populations III and IV combined. Appendix II presents, in numbers, the geographical differences within the groupings of Fig. 8. Population I trees are separated into equal samples from the Rocky Mountains north and south of the Arkansas River. The differences are marginal and probably of little significance. Larger samples and more detailed sampling might have shown more. The two equal samples from Arizona are from one locality, Mt. Agassiz, Coconino County. The differences they exhibit both separately and collectively from the Rocky Mountain trees are possibly significant, but they require further study. The differences between the two Arizona samples indicate the magnitude of the variation from sample to sample at a single location and even from different samples from a single tree. These differences should constitute a warning against interpreting the results shown in Appendix II and Fig. 8 in any but a very broad sense. The differences between trees of Population II from California and those

Figures 4–7.—Fascicle and needle characteristics.—4. Spread fascicle from a Population I tree from Colorado showing prominent single groove at distal end of dorsal surface of uppermost needle. A closely spaced pair of grooves is visible between the two larger resin exudations on the same needle. Stomatal lines can be seen on exposed ventral surfaces.—5. Closed facsicle of a Population II tree from Carbon County, Utah, showing needles with two moderately spaced resin ducts.—6. Closed fascicle of a Population II tree from the White Mountains, Inyo County, California, showing needles with two widely spaced resin ducts.—7. Closed fascicle of Population III tree from the Sierra Nevada, Inyo County, California, showing typical needles with two resin ducts.

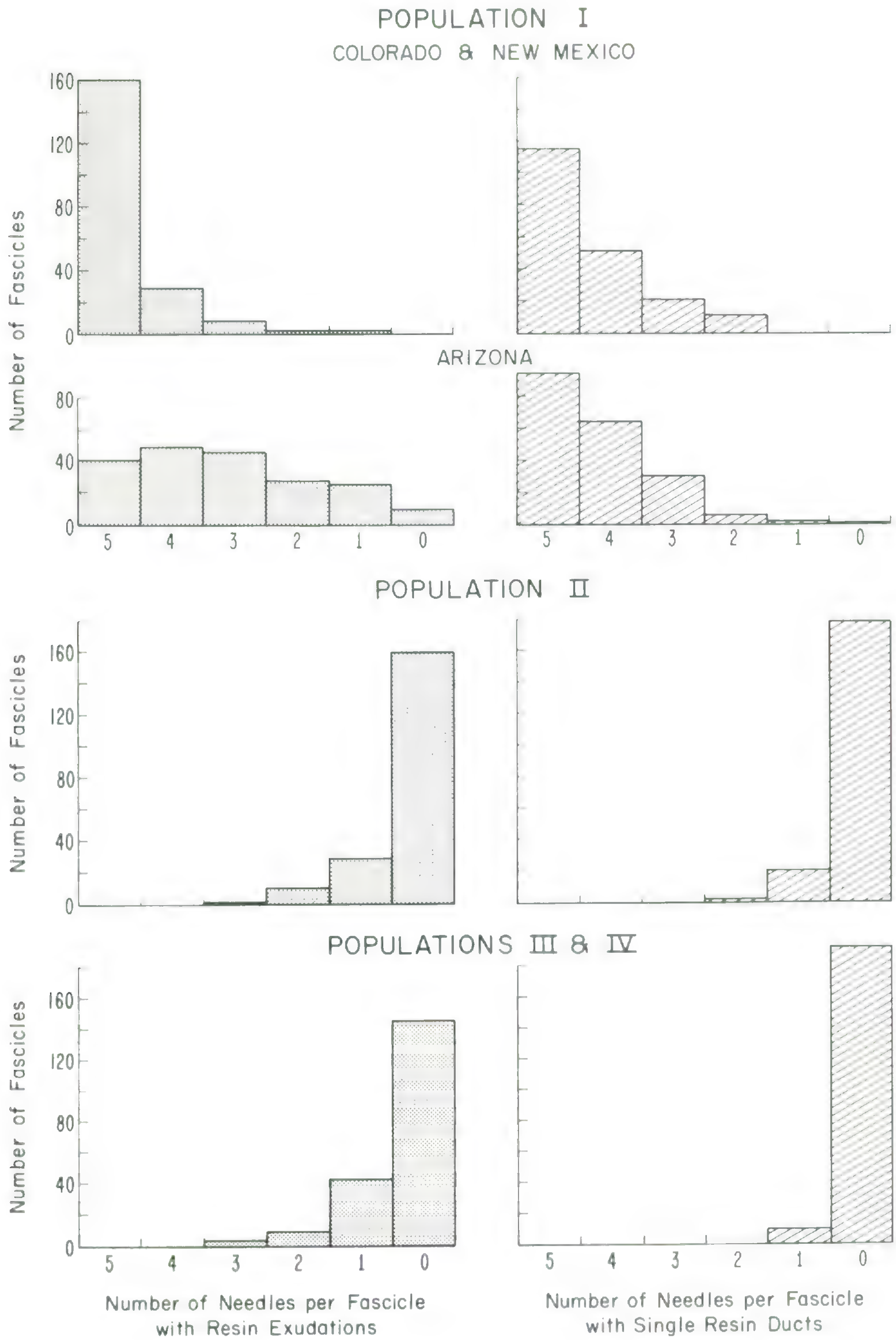


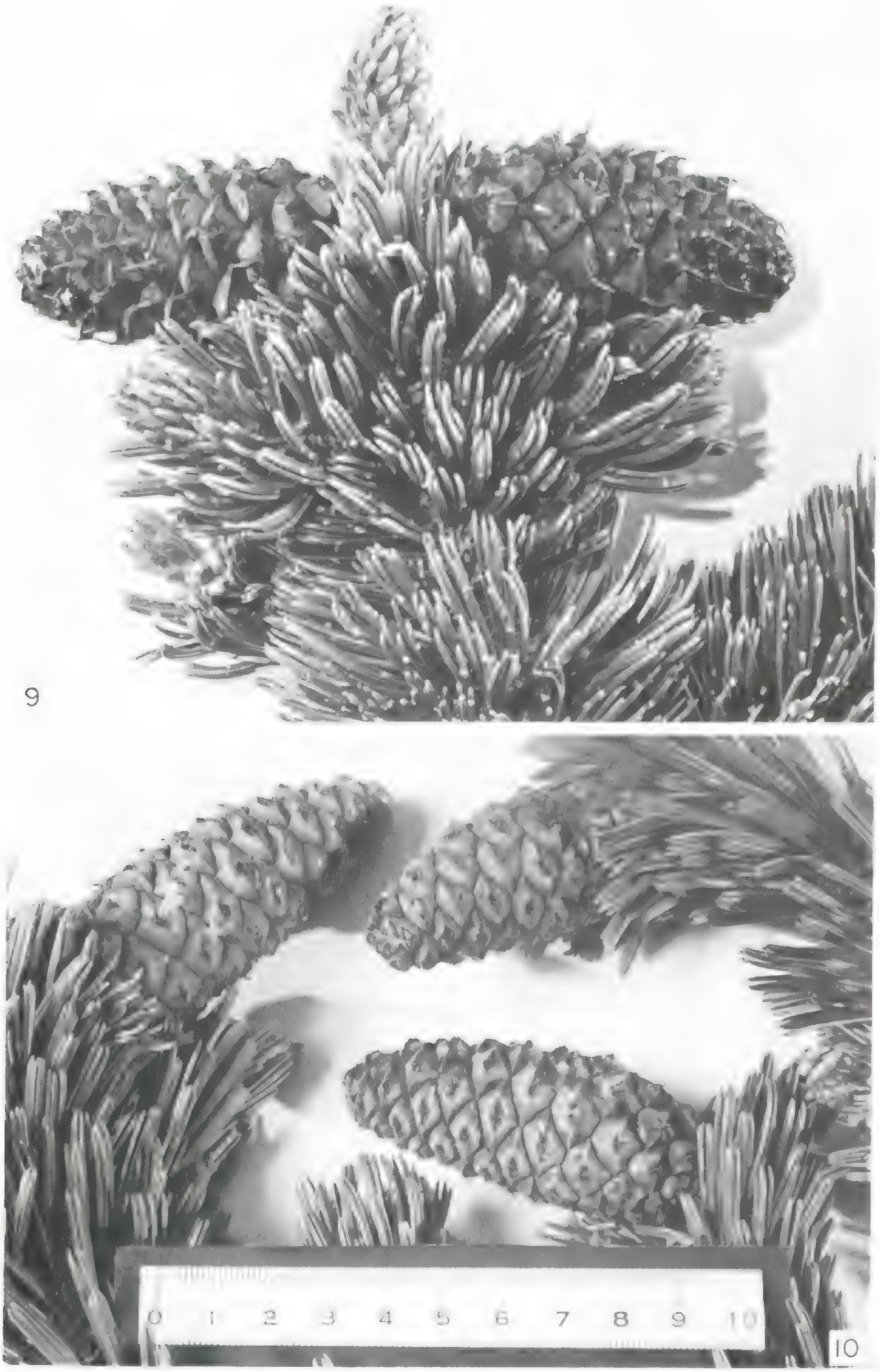
Figure 8.—Statistical distribution of needles per fascicle with one or more resin exudations, and with single resin ducts.

from Utah and Nevada are probably not significant, nor are the differences between trees of Populations III and IV.

As discussed earlier, high variability in resin exudation and duct characteristics exists mainly in Population I. To illustrate features of that variability, suppressed in the preceding analysis, Appendix III is supplied. The specimens of Appendix III are not randomly selected. For example the first specimen was chosen to show the maximum "dandruff" condition encountered, in the sense that every needle had at least one resin exudation, and the last specimen to show the least. All resin exudations on a needle are taken into account and in relation to their position along needles which, while terminating with a single resin duct, have more than one duct along some or all of the proximal three-fourths of their length. The resin exudations are said to be proximal or distal, according to where they occur with respect to the position at which the last duct, except for the terminating single duct, ends. In the previous analysis a needle was counted as having a single duct if it possessed a single duct for at least its distal quarter. In Appendix III the corresponding counts are represented by the sum of the number of needles having a single duct for their entire length and the number terminating in a single duct. These sums show comparatively little variation from sample to sample, but the numbers which are added from other lines in the Appendix to arrive at the sums, vary over a five to one range for needles with single ducts for their entire length and by more than twelve to one for needles terminating in a single duct. The frequency of occurrence of needles having two resin ducts along their entire length is also comparatively stable. It shows a variation of about three to one, and in this character the Arizona trees are in no way different from the trees of Colorado and New Mexico. The Arizona trees sampled do differ, however, not only in exhibiting fewer resin exudations but also in having fewer needles with single ducts for their entire length. The Arizona trees will obviously repay further study particularly using material from locations other than Mt. Agassiz. Herbarium specimens from other locations suggest that the differences reported above may be exaggerated.

Some additional foliage differences exist among the distinct populations. They have not proved amenable to any simple statistical approach and will only be discussed in descriptive terms.

Fascicle Spreading.—Compared with most pines, the members of the foxtail-bristlecone complex exhibit little spreading or splaying of the needles from the fascicle sheath. Trees of Population I spread or splay their needles the most of the four populations, although often not until the needles are two or more years old. The visual effect along branches is that of a soft brush. The fascicles of Population II trees tend to remain nearly closed for the life of the fascicle, and to be more appressed to the branch than those of Population I, so that the visual effect along branches is of a much coarser brush. Older fascicles usually open but not as much as fascicles of Population I. Trees of Populations III and IV seem to show even less tendency to spread their needles than those of Population II. The above tendencies are often observable in herbarium specimens as well as in fresh material and can be seen for individual fresh fascicles in Fig.



Figures 9–10.—Fresh branch and cone specimens (at same scale).—9. Specimen of Population I from Clear Creek County, Colorado, showing blunt second-year cones with highly protuberant apophyses and umbos, stout bristles, and foliage with resin exudations and spreading fascicles.—10. Specimen of Population II from Carbon County, Utah, showing second-year green cones. The cone bristles are comparatively small, but were somewhat damaged during transportation.

Figures 11–12.—Fresh specimens showing spindle-shaped cones.—11. Specimens of Population II trees from the White Mountains, California (Inyo County), showing second-year cones both green and purple.—12. Specimen of Population III from the Sierra Nevada, California (Inyo County), showing greenish-purple second-year cones with comparatively small bristles.

4–7. Figure 4 exaggerates the effect. The tendencies are also evident in the fresh cone-bearing branches (Figs. 9–12).

Needle Retention.—The common name, foxtail pine, is an allusion to the appearance of branches resulting from the extraordinary needle retention characterizing subsect. *Balfourianae* and setting its members apart from all other pines. Needle retention is most easily observed and the needles dated on branches that have persistently produced male strobili over a consecutive series of years. Such a branch with conspicuous annual gaps where the male strobili have been shed is shown in Fig. 13. Trees of Population I exhibit needle retention for about 10 to 15 years quite commonly, but very rarely for 20. Trees of Population II often exhibit needle retention for 25 to 30 years, and the author has collected a branch from a tree in the Snake Range, White Pine County, Nevada, with needles about 38 years old and still green and apparently capable of photosynthesizing. Needle retention in Populations III and IV, while obviously considerable, has not been closely examined in this study.

Needle Color.—Trees of the foxtail-bristlecone pine complex generally have darker foliage than that of the frequently associated limber pines, *Pinus flexilis*, and can be easily picked out by this difference among trees in a distant mixed stand. Color photographs show the difference clearly. Trees of Population I, however, seem darker and less yellow-green than those of Populations II and III. Field examination of trees of Population IV has not been made.

Figure 13.—Easily datable needles on a male branch of a Population II tree in the White Mountains, California (Inyo County). The year 1960, indicated by the pen, was a year of low available moisture as can be seen from the very short needles. Photograph made in June 1969 before the needles of that year had developed.

FOLIAGE—INTERNAL FEATURES

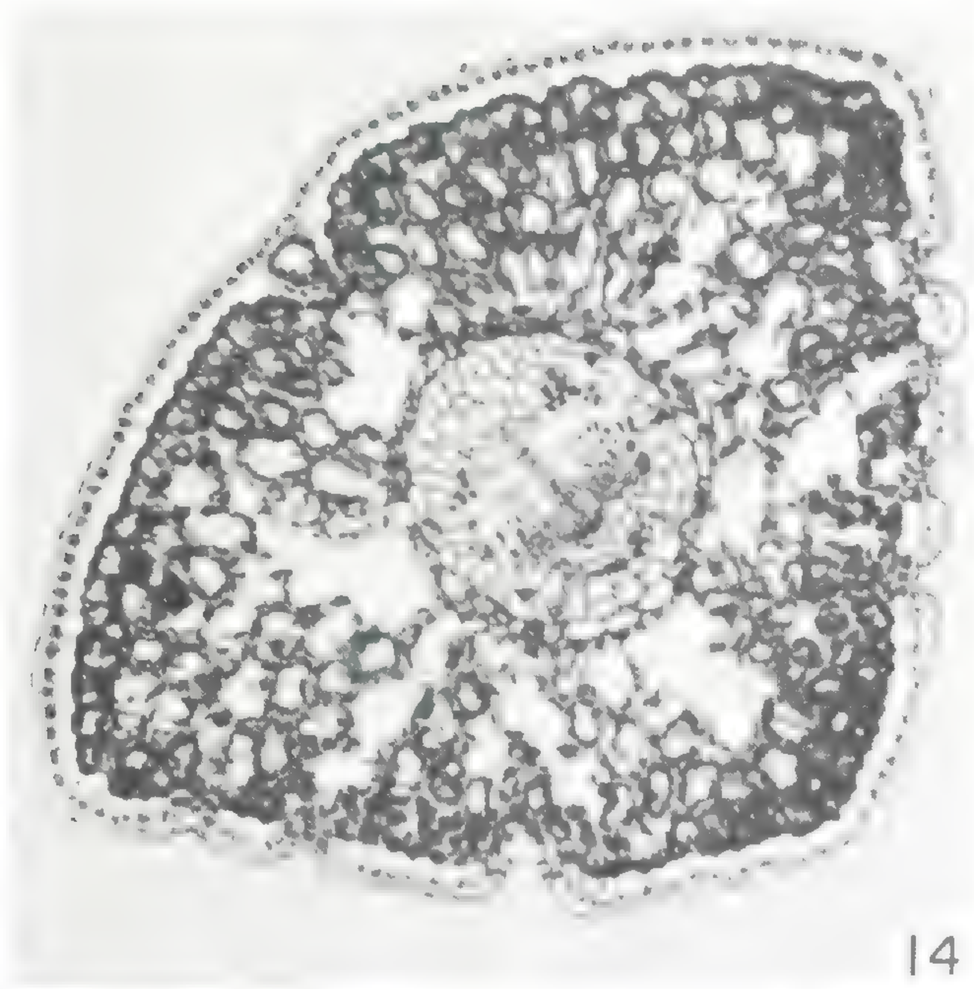
Shaw (1914) and Harlow (1931) provide drawings and photographs respectively of much magnified pine needle cross sections. Shaw shows *Pinus aristata* with a single resin duct but no overlying groove. Engelmann's drawings show the groove (Engelmann, 1863). Harlow illustrates *P. aristata* with two resin ducts, one very much smaller than the other, and both with overlying grooves. Despite its deficiencies Shaw's drawing must be taken to represent Population I. Harlow's photograph certainly does. Both Shaw and Harlow show *P. balfouriana* with two resin ducts of approximately equal size and no overlying grooves. Shaw, however, shows the ducts of *P. balfouriana* to be somewhat smaller in diameter than those of *P. aristata*—an obvious oversight, since they are in fact conspicuously and consistently larger. Apparently neither Shaw nor Harlow examined needles of Population II.

The groups of Figs. 14–19 and 20–25 show needle cross sections, magnified by somewhat varying amounts, of trees from Populations I and II respectively. Figures 26–31 show needle cross sections from trees of both Populations III and IV also somewhat irregularly magnified. The comments which follow are given by populations.

Population I.—Figures 14–18 represent Colorado trees; Fig. 19 represents an Arizona tree and confirms the earlier finding that Arizona trees belong to Population I. Figure 15 is an enlargement of the single resin duct shown in Fig. 14. Besides showing the characteristic overlying groove, it shows the conspicuous epithelial cells lining the resin duct. Figure 16 shows a needle with two ducts. Figures 17–18 provide the explanation of the resin exudations or "dandruff." The thin partition between the resin duct and the dorsal surface of the needle has ruptured allowing the needle to leak.

Population II.—Figure 20 represents a tree from Wayne County, Utah; Figs. 21–23 represent trees from Clark and White Pine Counties, Nevada. Figure 24 is from a tree in the White Mountains, Inyo County, California. Figure 25 shows in more detail a remarkable, deeply placed resin duct of the specimen of Fig. 22. Particular note should be taken of the size of the resin ducts, the inconspicuous epithelial cells, and the sclerenchymatous hypoderm cells surrounding the resin ducts. The partition of cells separating a resin duct from the needle surface is variable in thickness, ranging in the figures from the thick partition shown in Fig. 25 to the shallow ducts with thin partitions of Fig. 21. The latter cross section not only fails to exhibit overlying grooves, but even suggests the presence of ridges.

Population III.—Figures 26–28 and 31 represent needle cross sections of trees from the Sierra Nevada of California. In general these cross sections closely resemble those of trees of Population II, even to the variation in depth of the resin ducts. Figure 28 represents a needle from a specimen whose exact provenance could not be learned, although the branch specimen from which it came was supplied for this study in a fresh condition. The branch was notable in having more than twice the frequency of resin exudations found typical for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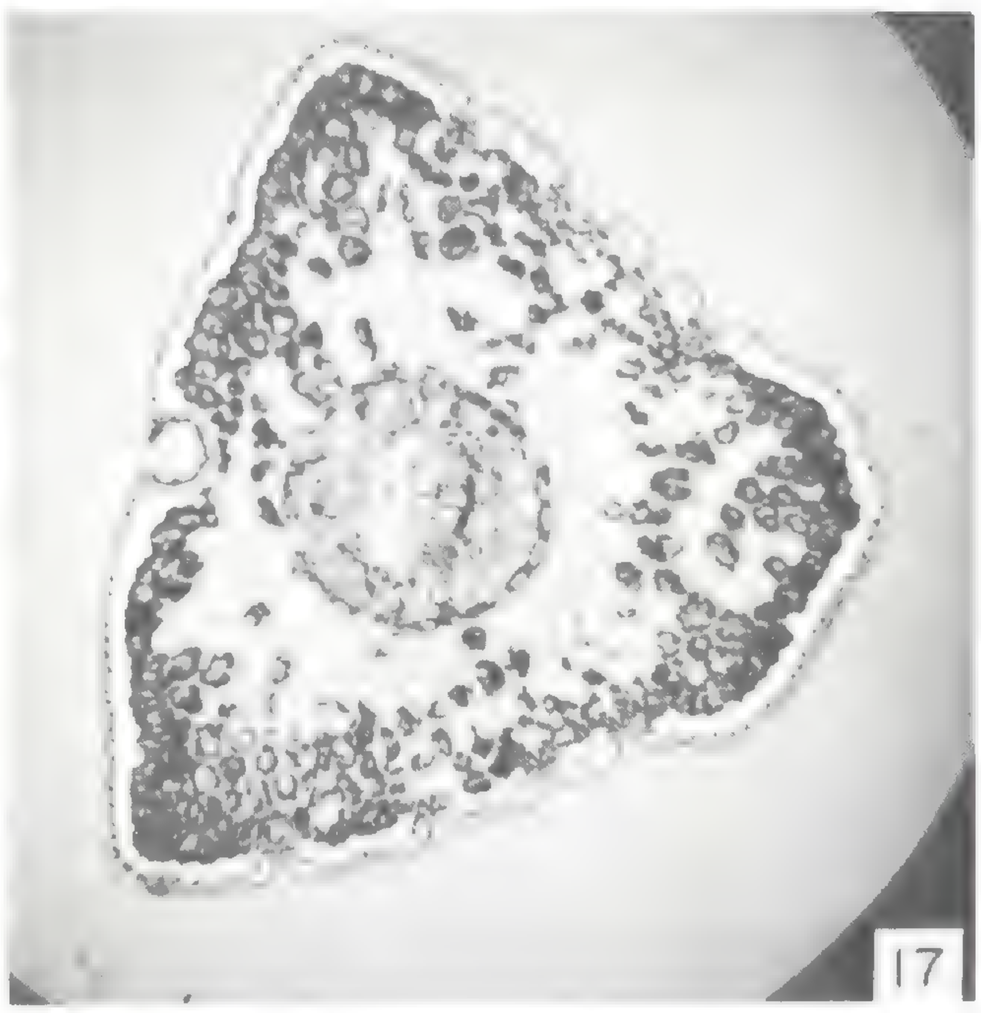
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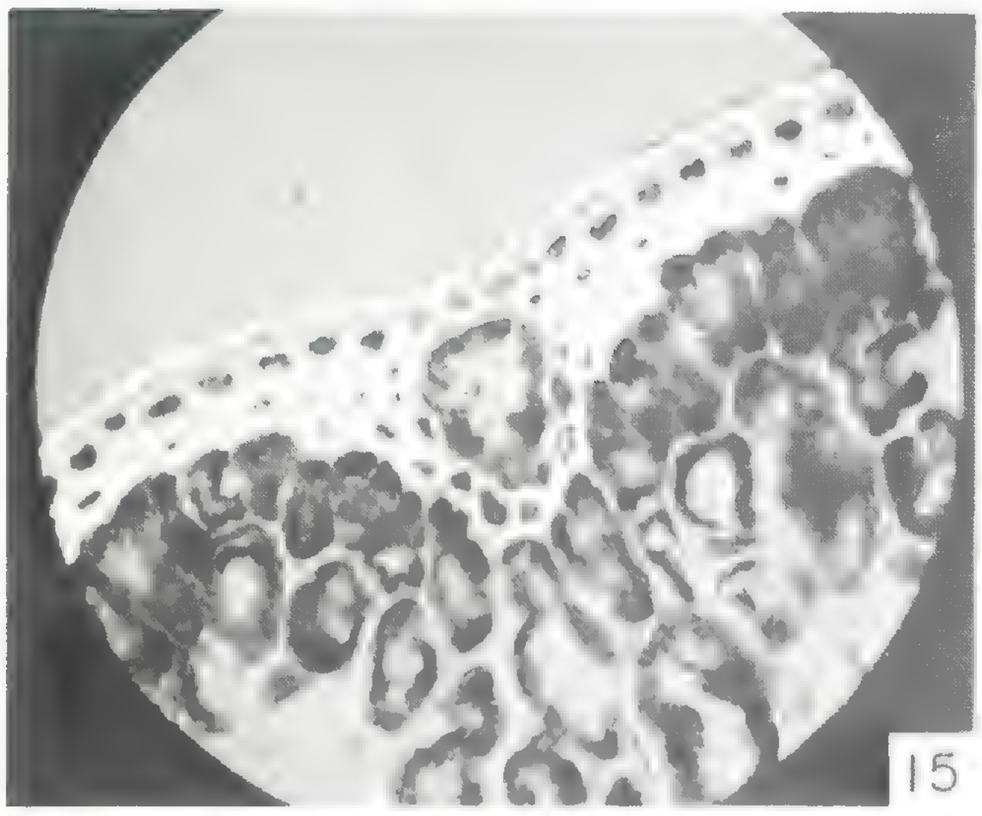
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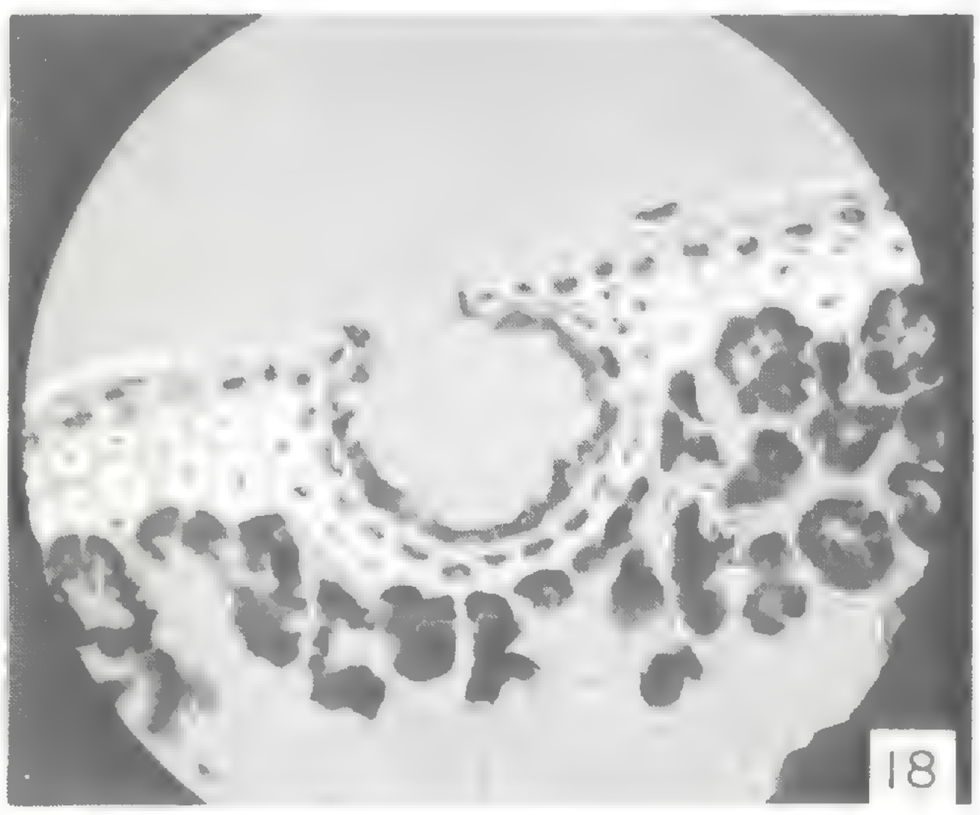
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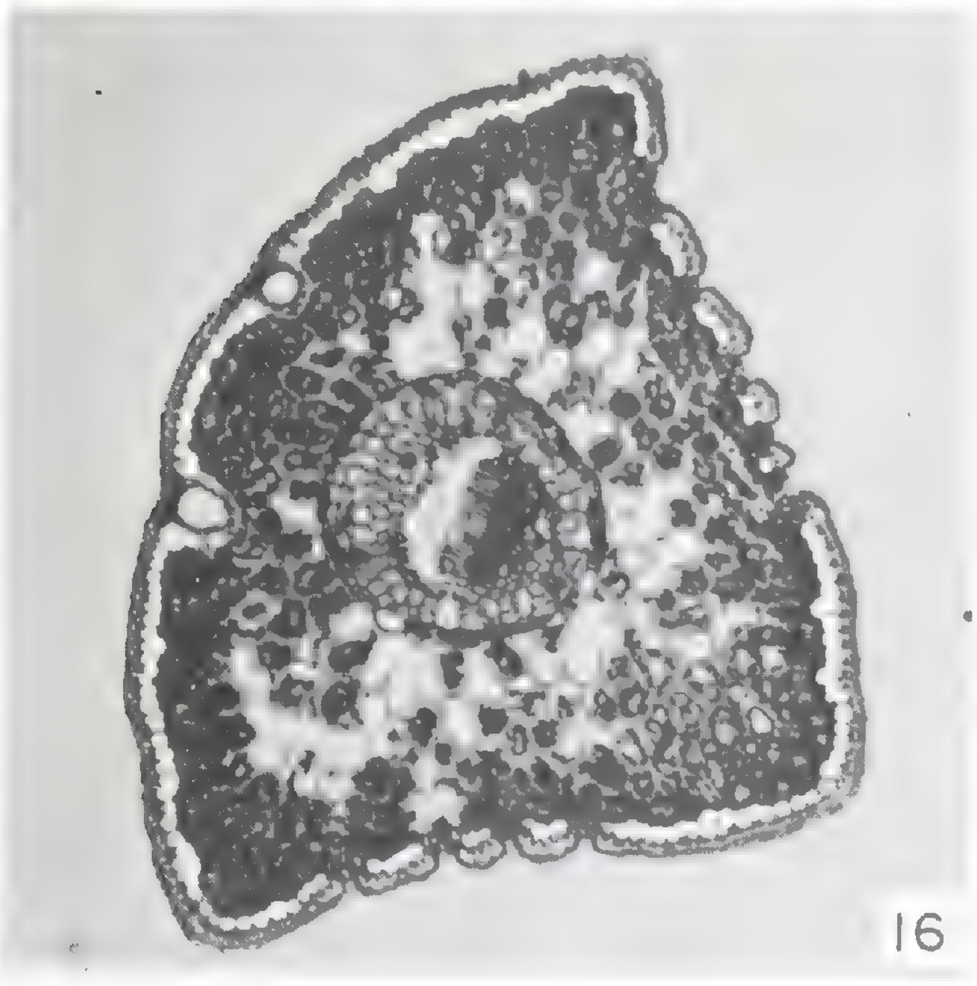
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Population III trees, and the reason seems clear from the needle cross section which shows large ducts very close to the needle surface. Figure 31, made from a slide provided by R. J. Mastrogiuseppe (personal communication, 1970), shows a needle cross section from a tree on Alta Peak, Tulare County, California. It is of interest in that the deeper of its two ducts is medial rather than external, being entirely surrounded by mesophyll. This is shown clearly by the unreproducible staining of the section itself.

Population IV.—Figures 29–30 represent needle cross sections from a tree on Mt. Eddy in Siskiyou County, California. This lone example exhibits no characteristics that distinguish it from a Population III needle. As with Populations II and III the epithelial cells are inconspicuous compared with Population I, and the two resin ducts are of approximately the same size, unlike those of Population I.

The needle cross sections of Figs. 20–31 show that internal needle characters at first glance are little better than external ones for distinguishing Population II trees from trees of Populations III and IV, whereas needles from Population I trees can always be distinguished from the others, both by internal and external characters.

There is, however, a minor difference of somewhat uncertain significance between Population II and Populations III and IV. It will be noticed in the figures showing needle cross sections that the resin ducts of Population II trees seem slightly larger in relation to the width of the ventral needle surfaces (approximately the radius of the fascicle) than the ducts of trees of Populations III and IV. This observation was tested quantitatively with the cross sections illustrated, together with a few additional cross sections made for the author, and the cross sections shown by Harlow (1931) and by Mehringer and Ferguson (1969). The procedure consisted of dividing the estimated fascicle radius (approximately the needle thickness) by the maximum dimension of the larger of the two ducts of the cross sections or the single ducts of Population I trees. It thus avoided concern with the varying enlargements of the available cross sections. The results of this sampling are averaged and given together with the probable errors of the averages in Table 1. The differences among populations would undoubtedly have been found to be very similar, if it had been possible to obtain and use actual dimensions of the ducts alone. Table 1 is interpreted as showing that resin ducts of trees of Population I are only about half the size of the ducts of the other populations, when measured relative to the size of the needle cross section. The result is highly significant. The table also shows, interestingly, that the resin ducts of trees of Population II are larger than those of Populations

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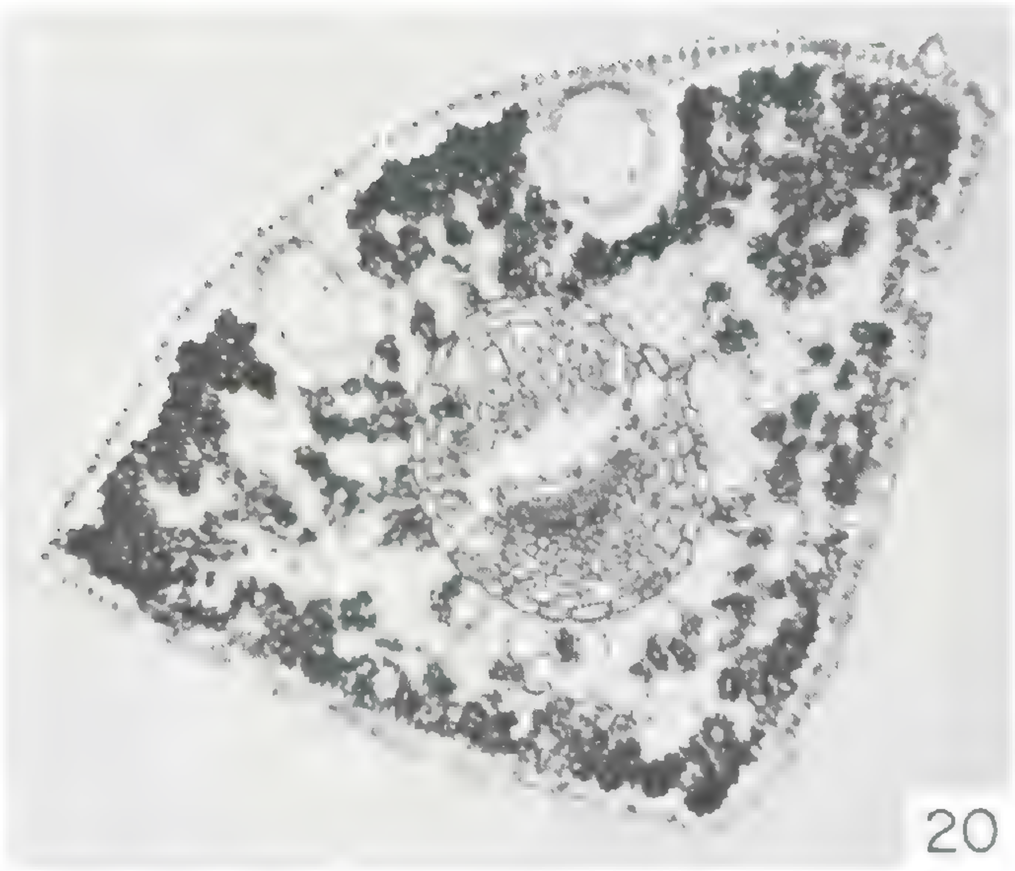
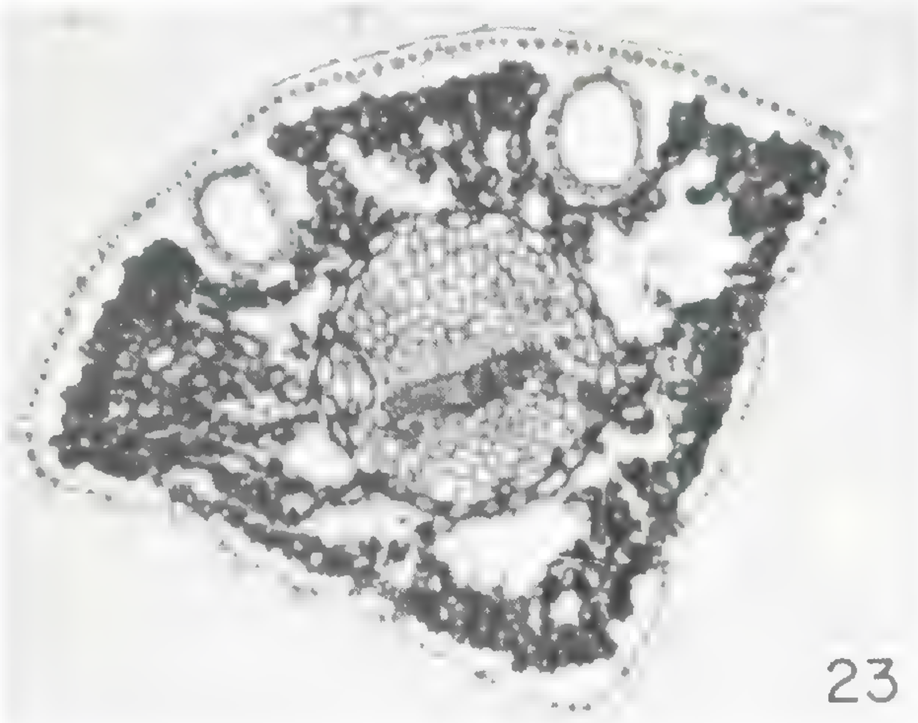
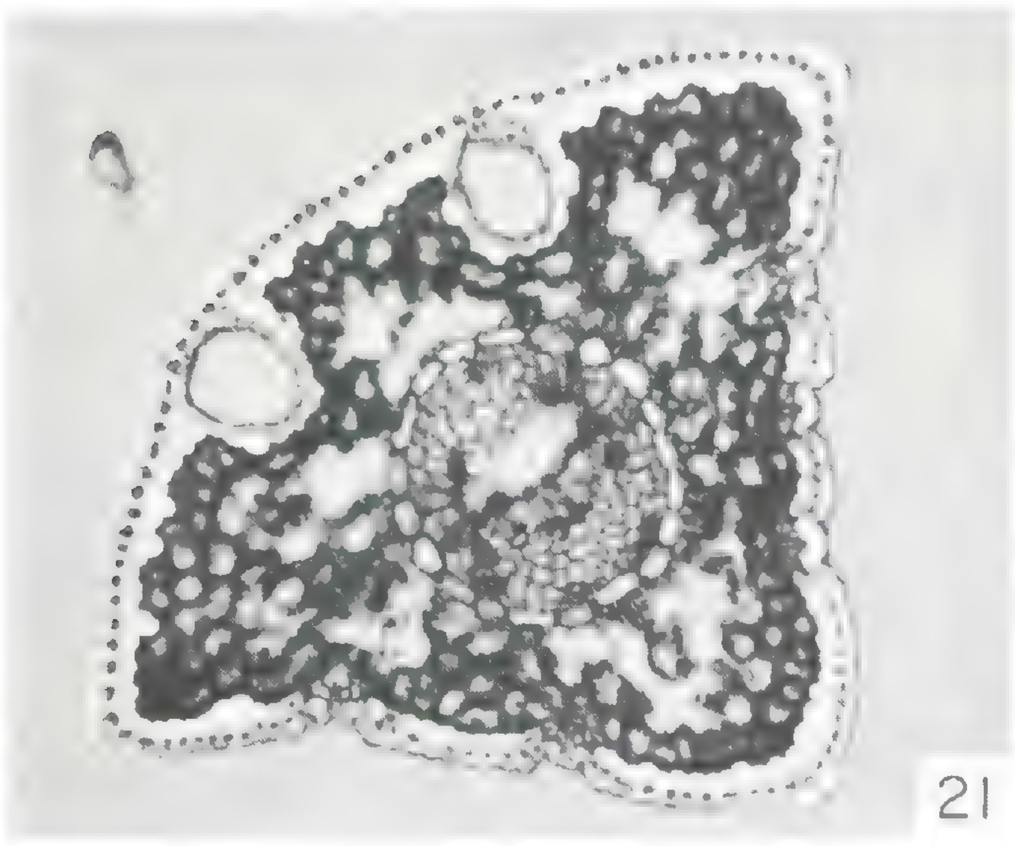
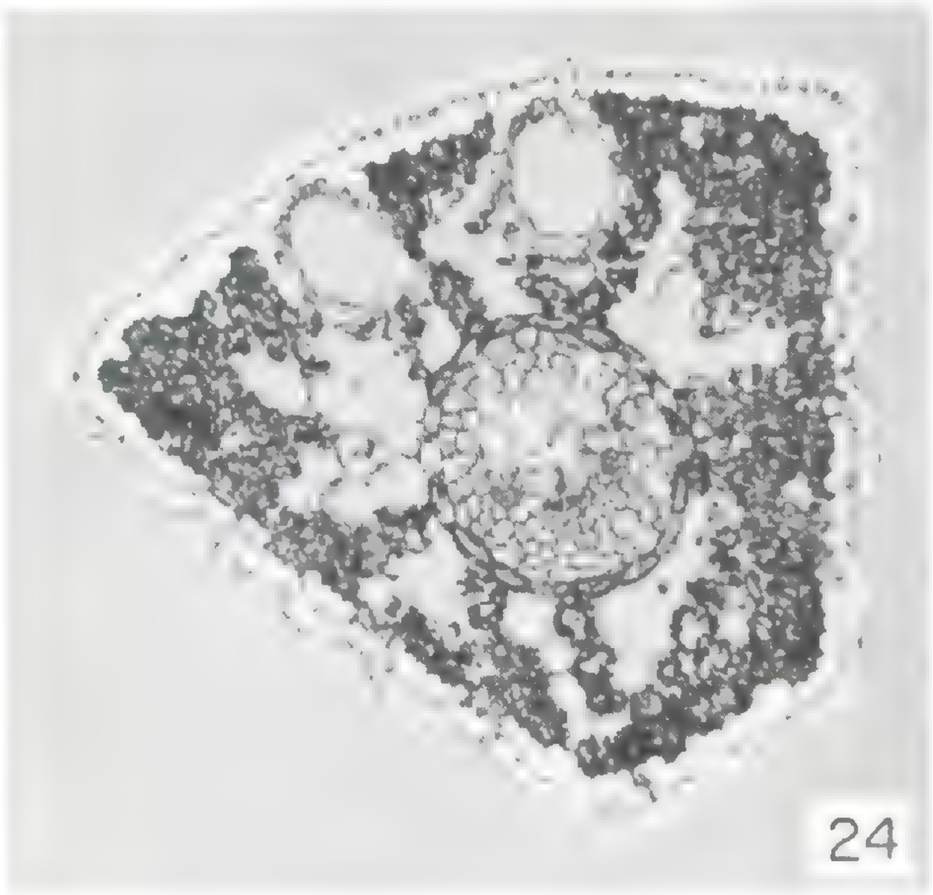
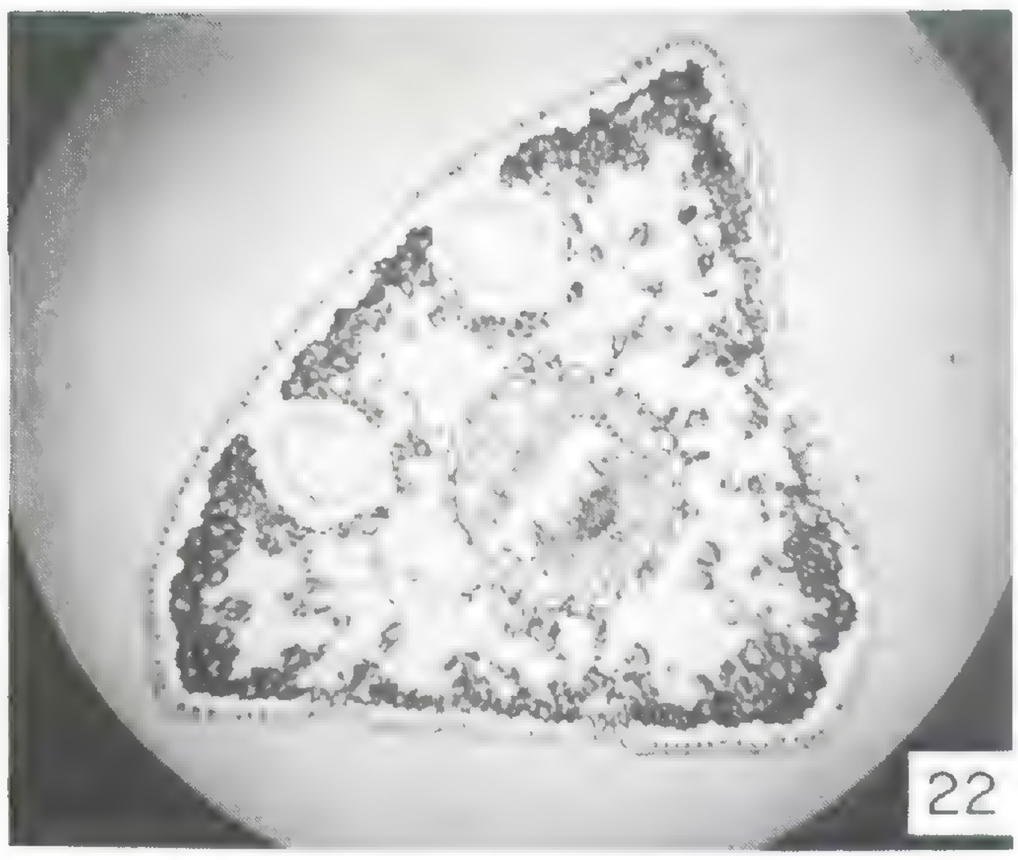
Figures 14–19.—Needle cross sections from trees of Population I.—14. Single resin duct beneath shallow groove (Clear Creek County, Colorado).—15. Enlargement of duct and groove of preceding figure.—16. Two resin ducts, each beneath a groove (Clear Creek County, Colorado).—17. Section through position of a resin exudation showing ruptured resin duct.—18. Enlarged view of the ruptured resin duct of the preceding figure.—19. Single resin duct beneath shallow groove from Arizona population (Coconino County).

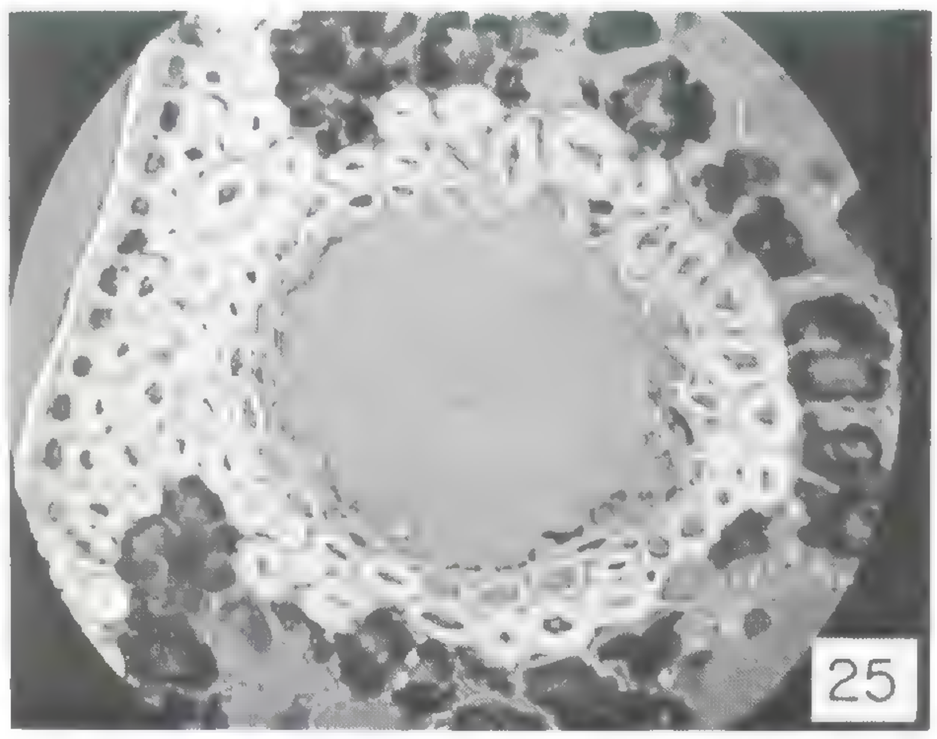












Figures 20–25.—Needle cross sections from trees of Population II.—20. From southern Utah (Wayne County).—21. From southern Nevada (Clark County). 22. From eastern Nevada (White Pine County) with very thick resin duct walls.—23. More typical specimen from same locality as preceding figure.—24. From White Mountains, California (Inyo County).—25. Enlargement of duct of Fig. 22.

TABLE 1. Resin duct sizes.

Population	Number of cross sections sampled	Ratio of fascicle radius to duct diameter: Average	Ratio of fascicle radius to duct diameter: Probable error of average
I	11	14.1	±0.46
II	15	6.3	±0.14
III & IV combined	12	9.0	±0.40

III and IV. This second finding has less statistical significance, but it is probably real. When it is applied to the cross section shown by Mehringer and Ferguson (1969) in their Fig. 5G, it confirms that their dried needle from a late Pleistocene wood-rat midden found on Clark Mountain in the Mohave Desert is indeed from Population II, or what they call *P. aristata,* rather than from *P. balfouriana* —a fact they only assume in the absence of either species on the mountain at the present time.

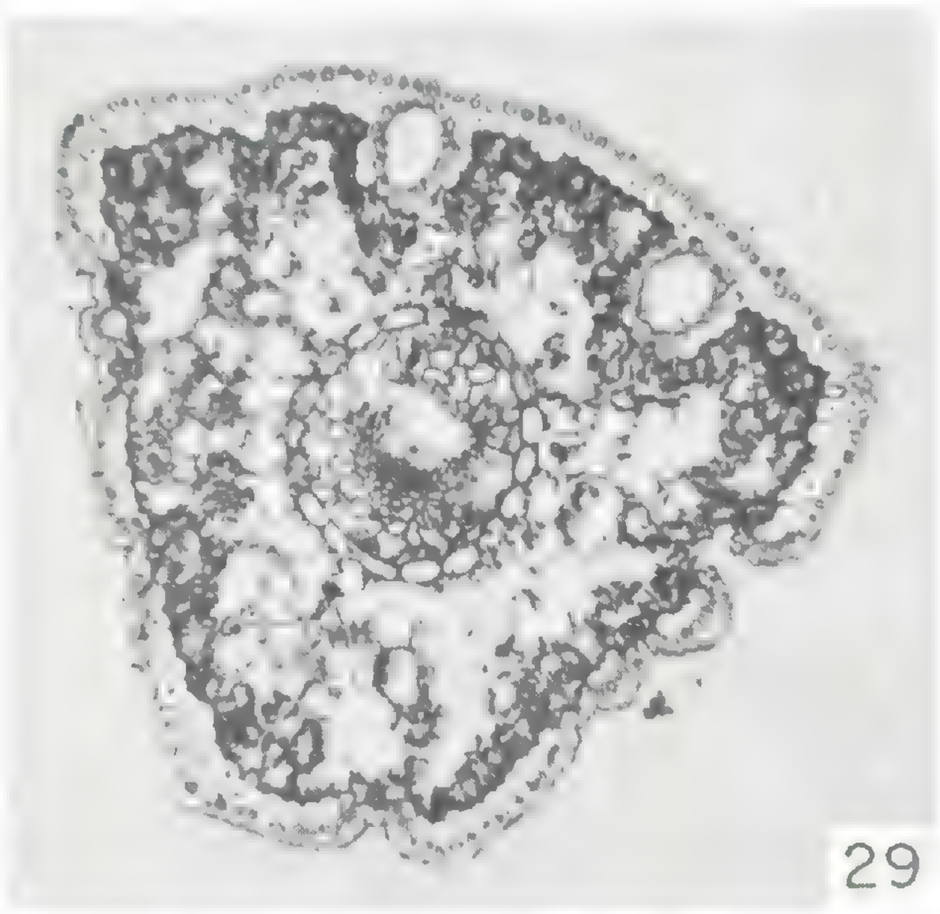
To terminate the discussion of internal needle characters, and mainly of resin ducts, it should be noted that the relative size of the ducts of trees of Population II is among the largest of all the pines, whereas the ducts of trees of Population I are comparatively small, though not the smallest.[7] For two populations obviously so closely related this is very surprising, especially when it is realized that these characters are highly stable in each population.

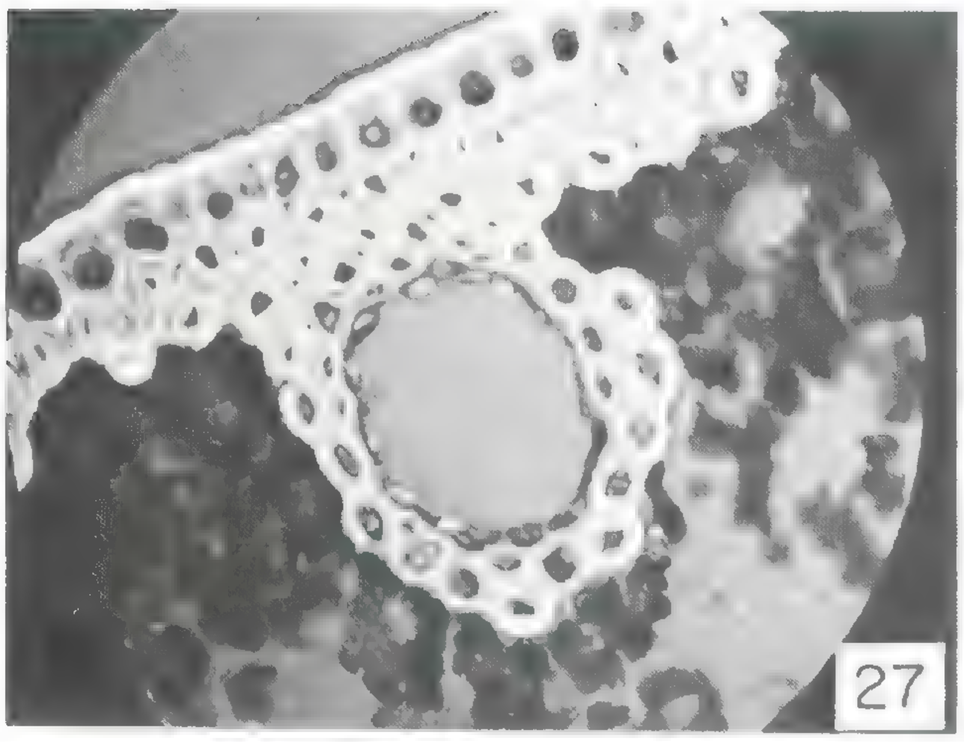
REPRODUCTIVE PARTS

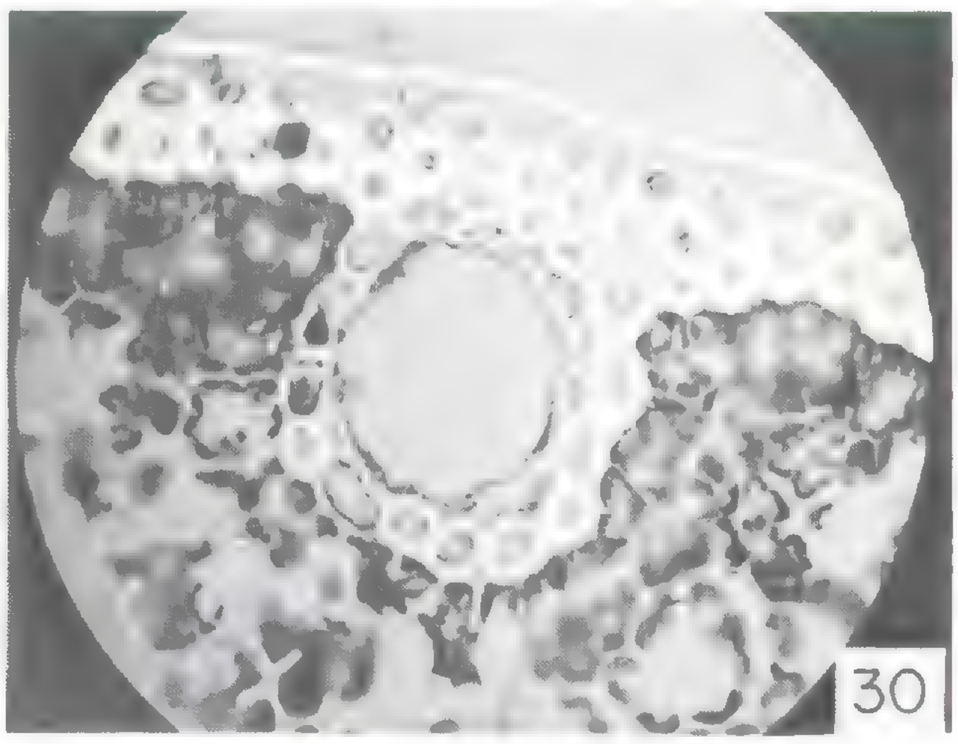
Cones.—Cones are notoriously variable in pines (*cf.* Griffin, 1964). However, some progress can be made in identifying differences among the cones of the four populations. Populations III and IV, considered together, have been distinguished customarily from Populations I and II, also customarily considered together, by having distinctly fewer cone scales, rather fleshy apophyses, and minute bristles. Also frequently they have a pronounced curvature of the cone axis, though this is rarely mentioned. It is equally customary to consider that the ripe cones of Populations I and II are identical, within what is considered to be their normal variations, and of a more ovoid shape than cones of Populations III and IV.

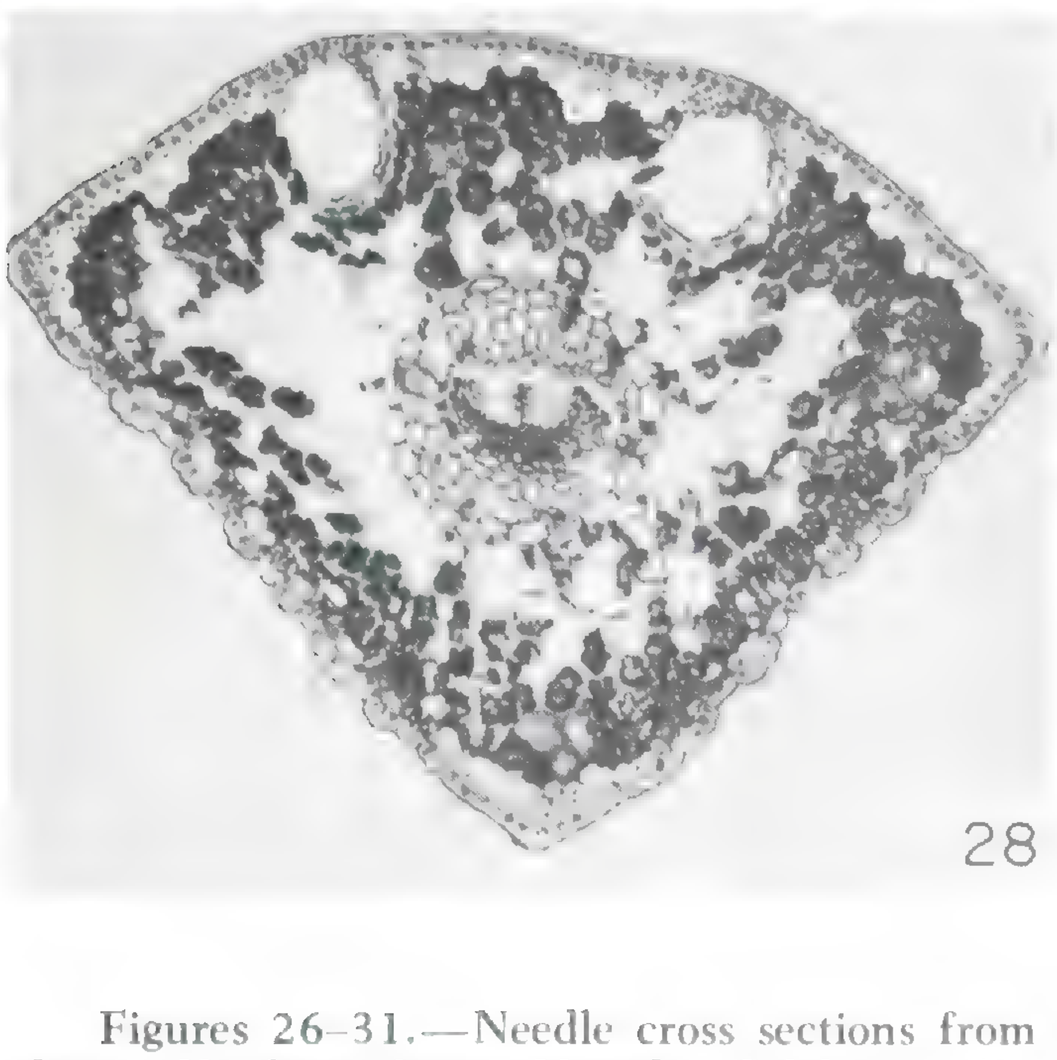
Figures 32–33 illustrate the above generalizations with regard to ripe cones, and Fig. 32 serves to identify other kinds of differences. For example, cones of Population I trees have a very high frequency of flattened bases—so flat that they can usually stand on their ends; occasionally their bases are reentrant. Population II cones are much more rounded at their bases, and examples can only rarely

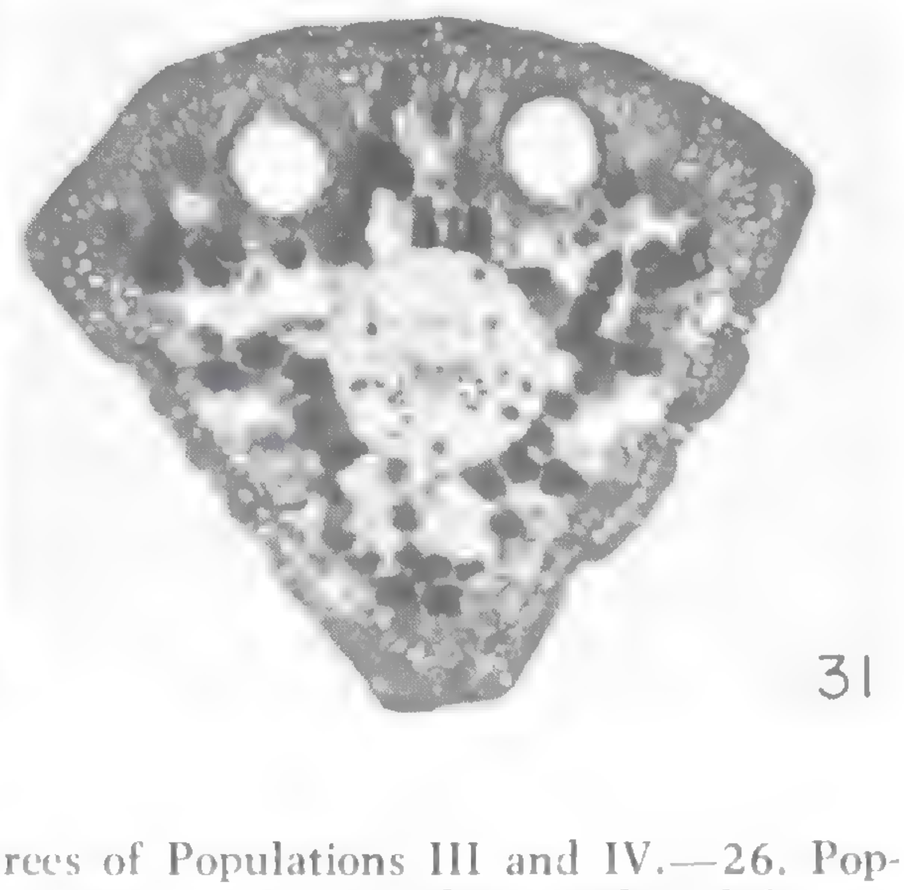
[7]Population I trees are also almost but not quite alone among pines in possessing mainly single resin ducts. *Pinus culminicola* Andresen & Beaman, a recently described rare 5-needle pinyon pine from Mexico, possesses almost entirely single external resin ducts with no overlying grooves and no resin exudations. Like trees of the foxtail-bristlecone pine complex, *P. culminicola* has stomatal lines only along the ventral needle surfaces.











Figures 26–31.—Needle cross sections from trees of Populations III and IV.—26. Population III from Sierra Nevada, California (Inyo County). Ignore photographic defect in resin duct at left.—27. Enlargement of resin duct from another cross section of preceding needle specimen.—28. Population III from another collection from the Sierra Nevada. Resin duct at left is exceptionally close to needle surface.—29. Population IV from Mt. Eddy, California (Siskiyou County).—30. Enlargement of resin duct from another cross section of preceding needle specimen.—31. Population III from Alta Peak, California (Tulare County). Resin duct at left is medial.

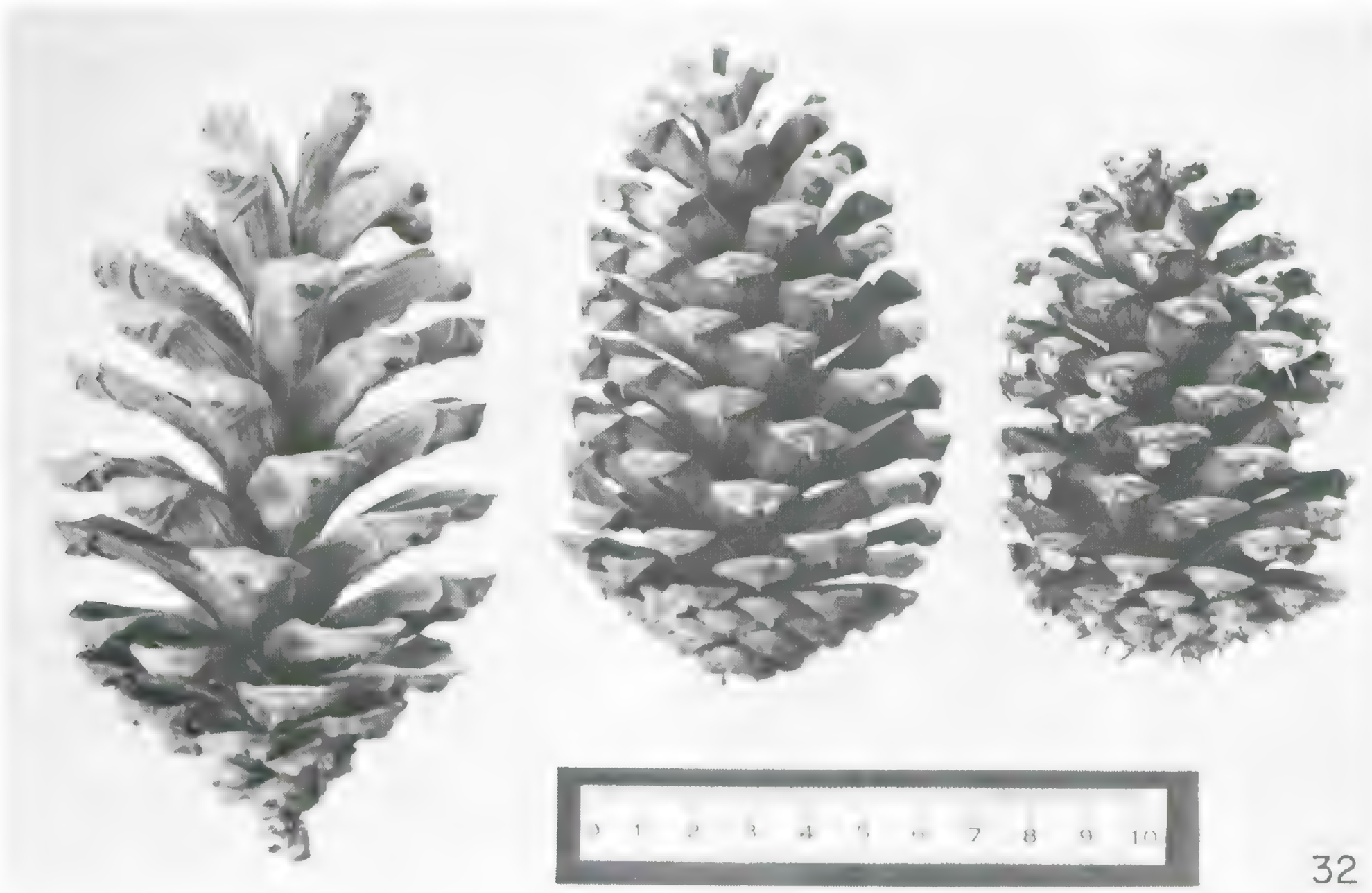
TABLE 2. Gross cone statistics.

Population	Number of cones sampled	Average number of scales	Probable error of average	Average length of cone, cm	Probable error of average, cm
I	40	108	±1.9	8.0	±0.15
II	40	117	±1.7	9.1	±0.14
III	25	83	±1.9	8.7	±0.25
IV	15	79	±2.0	9.3	±0.32
III & IV combined	40	82	±1.4	8.9	±0.20
(Mastrogiuseppe's Results)					
III	537	80.7	—	7.8	—
IV	540	81.1	—	9.5	—

be found that will stand on end. Population III and IV cones have pointed conical bases, and examples can almost never be found that will stand on end. Cones of Population I are very resinous and sticky to handle. Cones of Populations II, III, and IV are much less resinous. The bristles of Population I cones are both stout and long, and tend to stick outward from the cone axis so that grasping the cone can be a painful experience. Cones of Population II trees usually have finer and shorter bristles that tend to be recurved when ripe. The bristles at the base of cones from Population I are particularly stout and prominent, whereas those at the base of cones of Population II are small and often missing. The comparatively short bristles of cones of Populations III and IV are fine, and many are lost by the time the cones reach maturity. They are often broken off in herbarium specimens.

Significant color differences are found among ripe cones that have experienced only brief weathering. Population I cones are buff to gray-brown and occasionally slightly reddish, whereas those of Population II are usually a rich rusty reddish brown and not very different in color from fresh cones of Population III. Fresh ripe cones of Population IV trees have not been examined but are believed to be less reddish.

An attempt has been made to obtain gross statistics of cone scale numbers and cone lengths with the results shown in Table 2. While cones of Population II tend to be somewhat longer and to have somewhat more scales than cones of Population I, the significance of the differences is doubtful. It would appear that cone shape, bristle form and distribution, and color constitute better distinguishing characters of ripe cones than length and number of scales. The author has tested his ability to distinguish between cones of Populations I and II by examining herbarium specimens with the labels hidden. He found that he could quickly and correctly identify cones in more than 90 percent of the cases without taking dimensions or scale numbers into account. Differences between Populations III and IV are less significant. The results do, however, confirm the significantly smaller number of scales in cones of Populations III and IV compared with Populations I and II. Populations III and IV are at present under intensive study



Figures 32–33.—Ripe cones.—32. From left to right cones of trees of Populations III, II, and I.—33. Cone variation, two Population III cones, one with 73 scales (at left) and the other with 103.

as a thesis topic[8] on geographical variations by R. J. Mastrogiuseppe (personal communication, 1970). Mastrogiuseppe, in his statistical studies of cones, has used very large samples. Some of his results—privately communicated to the author—are shown with permission for comparison in Table 2. Figure 33 illustrates how scale number can vary between two cones of the same population and same length.

Unripe second-year cones, so much in evidence during the brief summers experienced by the trees of the foxtail-bristlecone pine complex, exhibit other character differences of particular importance in distinguishing between Populations I and II. These differences are clearly shown in Fig. 9–11. In Figure 9, showing a fresh cone and branch specimen of Population I, the long stout bristles are evident. Figure 9 also illustrates the bluntness of the cones and the highly protuberant apophyses and umbos, which do not characterize cones of Population II. The cones of Fig. 10 and the left-hand cone in the group of Fig. 11 are examples of the so-called green cones of Population II, that are actually brilliant yellow-green. The cones at this phenological stage are usually purple. This color distinction among cones seems to occur only in Population II and is genetic in nature. Thus cone color is associated with an entire tree. Trees producing green cones are rare, probably considerably less than 1 percent in any given sample of trees. Green cones are found throughout the geographical range of Population II[9]. The cones in Fig. 11 illustrate well the long tapering form found in Population II. These cones may be referred to as spindle-shaped, as distinct from the ovoid cones of Population I. Cones of Population III are shown in Fig. 12, which illustrates the close similarity in shape of unripe cones of Populations II and III. It also illustrates the smaller bristles and the fewer cone scales. Unripe second-year cones of Population IV are very similar to those of Population III.

Male Strobili.—Distinctions among the four populations with respect to male strobili have not been much searched for and are certainly not great. Male strobili of Populations I and III, when just starting to shed pollen, are of a rich pure yellow. As they reach the end of pollen shedding, they darken into a light orange-brown. Male strobili from most trees of Population II, observed thus far only in the White Mountains, Inyo County, California, have a distinct rather variable purplish pink blush. In this region the rich pure yellow male strobili seem to occur only on trees bearing the green cones discussed earlier. Not quite fresh, but nearly ripe, male strobili from Population IV trees suggest similarity with Population III. While male strobili require further investigation, it appears that Population II stands distinct, insofar as the purple-cone bearing majority of its members is concerned, by having distinctively colored male strobili.

It is inappropriate to discuss pollen inasmuch as insufficient information is at present available. Pollen from trees of Populations II, III, and possibly IV has been microscopically studied in connection with the identification of fossil

[8]For Humboldt State College, Arcata, California.

[9]The specimens in Fig. 10 came from Price Canyon, Carbon County, Utah. Unfortunately they were much less fresh, when photographed, than those in Fig. 11, from the White Mountains, Inyo County, California, and their color had somewhat darkened.

pollen (Axelrod & Ting, 1960). But these studies, because they have been based primarily on material from California and the Great Basin, do not appear to have included pollen from Population I trees.

Seeds.—Seeds, like pollen, require further study. Mastrogiuseppe (personal communication, 1970) has shown that the seed wings of Population IV trees are systematically longer by about 50 percent than those of Population III. The seeds themselves are also about 25 percent longer. It seems, from much more limited sampling, that seeds and seed wings of Populations I and II are of roughly the same size but somewhat smaller than those of Population III. In all populations the seed is usually somewhat mottled and the seed wings articulate. The seed coats of Population I seem to be considerably darker in color than those of Population II, but field work designed to allow more extensive and detailed comparisons is needed. Shaw (1914) is incorrect in stating that *Pinus aristata* can be distinguished from *P. balfouriana* by the seed wings—the former having articulate rather than adnate seed wings.

CHEMISTRY

The chemistry of the gum turpentines of trees of Populations II, III, and IV has been studied (Haagen-Smit *et al.*, 1950; Mirov, 1961) with interesting results. Surprising differences were found between Populations III and IV, both in chemical composition and in optical rotation. Trees from Population II in the White Mountains had a similar but not identical chemistry to trees of Population III and exhibited about the same optical rotation. The gum turpentines of trees of Population I have not yet been studied.

It has been found, without the benefit of quantitative chemical analysis, that the chemical differences between Populations I and II are great enough to provide, in the simple qualitative factor of odor, a useful diagnostic tool. Odor difference is particularly marked in freshly collected branch and needle specimens, the odors of which undoubtedly come mainly from needle and phloem resins. Population I trees have a strong, slightly spicy, pungent odor of turpentine. The quality of turpentine is entirely missing in similar specimens from Populations II and III. The latter two populations exhibit, in comparison, very little difference in odor. Their odors are much weaker and sweeter. Although completely fresh specimens of Population IV were not available, the odor of specimens not more than a few weeks old does not have the turpentine quality of Population I.

In the case of Population I material, the strong, almost unpleasant, turpentine odor seems to represent a highly volatile or an easily convertible fraction, since the odor weakens rapidly as specimens become dry. But it never disappears entirely and is still faintly discernable in long-dead resinous heartwood. With such wood, however, the odor difference between Populations I and II is much less marked.

As indicated earlier chemical differences between Populations I and II are probably involved in the differences in physical properties of the resin exudations and in differences in the colors of ripe cones. They are also possibly related to the color differences observed in old, weathered wood. In trees of Population I

the weathered wood is buff to drab grayish brown, with occasional traces of bright yellow or orange. Trees of Population II have paler weathered wood, suggesting slight pinkishness. The latter trees often show yellows and orange-browns in weathered wood of a brilliance rarely, if ever, found in Population I. It should be added that weathered wood of limber pine, *P. flexilis*, shows similar colors to Population II trees, though often somewhat grayer and with less suggestion of pinkishness. Coloring alone of long-dead trees near timberline, does not always allow certain identification of Population II trees. Weathered wood of Population III trees is very similar to that of Population II trees. Population IV trees have not been examined for weathered wood coloring.

GROWTH FORMS AND BARK

Differences in growth form, particularly the pendulous, twisted branching of Population II trees as compared with the more upright, fastigiate branching of Population I trees, were noted more than a century ago. These differences were discussed earlier and illustrated in Figs. 1–2. There is a tendency, particularly in the Population II stands of the White Mountains, for the larger trees on the better watered sites to occur in two very different forms. One exhibits the pendulous habit to such an excessive degree that the trees could be termed "weeping" in the same sense as weeping willows and weeping mulberries. The other form, while not weeping, is still pendulous. It exhibits long, unbranched "foxtails" twisted in many directions, which give the tree a grotesque, tortured appearance. When found side by side, the two forms provide a remarkable contrast. The same two forms are found in Population III trees of the eastern Sierra Nevada, but to a less marked degree. It might be thought that the pendulous habit of the Population II trees is a simple consequence of their greater needle retention and therefore heavier branches. This possibility may contribute to the habit, but it can scarcely account for the extreme forms.

Pinus balfouriana at maturity and when of large size tends commonly to be developed around its original and still living leader. However, ancient and much weathered specimens of Population III have been observed on dry granitic ridges. Such trees, which have suffered much cambial dieback, have long since developed multiple leaders to replace their original leader and are quite indistinguishable in general appearance from the ancient specimens of Population II in the White Mountains and in similar dry localities farther east.

Bark characteristics are highly variable in similar ways among the four populations. In Population III, however, a bark form has been observed occasionally that seems to be unique. It is exceptionally thick, perhaps 6–8 cm, and occurs in large squarish plates, with a very rich reddish brown color. Thin reddish bark and large, but brown "alligator" plates have been observed in Population I, but the striking combination just described has not. Population IV trees, although very closely related to Population III, have not been found with this kind of bark accordng to Mastrogiuseppe (personal communication, 1970).

TABLE 3. Longevity and precipitation.

	Estimated maximum attainable age, years	Typical annual precipitation [a] Total, cm	Distribution
Population I			
Colorado	2000	50–100	Summer maximum
New Mexico	2000	>40	Summer maximum
Arizona	1000	>75	Summer maximum
Population II			Summer and
Southern Utah	3000	50–75	winter maxima
Eastern Nevada	5000	>40	Winter maximum
California	5000	25–40	Winter maximum
Population III	2000	50–100	Winter maximum
Population IV	1000	150–200	Winter maximum

[a] Based mainly on information contained in U. S. Department of Commerce, Weather Bureau or Environmental Science Services Administration publications: *Climates of the States* and the *Decennial Census of United States Climates, Climatic Summary, Supplement for 1951 through 1960* as published for each of the six states of concern.

ENVIRONMENTAL CONSIDERATIONS

Pines of subsect. *Balfourianae* have adapted to climatic extremes in ways approached by very few other pines. Like all pines they are intolerant of shade. As a consequence their stands are never very dense, and only under conditions of environmental compensation do they grow to a limited extent among other high-altitude conifers. At their lower altitudinal limits they occasionally overlap the upper limits of the pinyons and *Pinus ponderosa* Laws. The ability of pines of subsect. *Balfourianae* to survive on very little moisture, and sometimes throughout prolonged drought conditions, is extraordinary. The latter conditions are imposed both by lack of much precipitation and by the very short growing season at the high elevations where the trees are found. Trees of subsect. *Balfourianae* do not succeed naturally at the lower elevations, where the pinyons flourish, because their requirements for water cannot be met. On well-watered sites below their natural lower altitudinal limits they are excluded by the competition mainly of other conifers. The higher temperatures of the lower elevations, alone, are not inimical to them, and under cultivation trees of both Populations I and II are known to do well at elevations far below their natural range, when supplied with adequate water and kept free of shading. The upper altitudinal limits are determined by the combined action of exposure to harsh drying winds often transporting abrasive material and shortness of the temperature-dependent growing season, not by total precipitation or low winter temperature *per se*. Thus at upper timberline bristlecone growth is highly temperature sensitive, whereas at the lower altitudinal limits the growth is precipitation sensitive (Ferguson, 1968; Fritts, 1969; LaMarche, 1969).

The great longevity attained in certain stands of the bristlecone pines of Population II is a result of several factors, not the least of which is very low annual precipitation with a pronounced winter maximum. Schulman (1954) discussed the longevity of conifers under adverse conditions. LaMarche (1969)

has discussed in considerable detail the characteristics of the environment, both climatic and edaphic, in relation to the growth habits of trees of Population II which contribute to their longevity. Table 3 indicates the estimated maximum attainable ages of the various populations of subsect. *Balfourianae* and typical precipitation characteristics of the different regions where they occur.

A great many of the known stands of trees of Population II are found growing on limestone or dolomite substrates. Wherever the substrate is, for example, granite, sandstone, or quartzite, to name some common rock types, the trees are fewer and they seem to experience severe competition with other trees. Thus on a granite substrate at the Crooked Creek Laboratory in the White Mountains at 3100 m, the surrounding open forest consists mainly of limber pine with only an occasional bristlecone. On the dolomite soils in the Schulman Grove a few miles to the south, the situation is reversed. The apparent affinity of trees of Population II for limestone and dolomite has been thought to be of an intrinsic nature. Population I trees on the other hand form fine stands on non-carbonate substrates in the Rockies and northern Arizona. Population III trees also thrive on non-carbonate substrates such as the granites of the Sierra Nevada. Wright and Mooney (1965) investigated the apparent preference of Population II trees in the White Mountains for dolomite, and they found it to be associated with physical properties of the substrate. Limestone and dolomite form relatively light colored soils which reflect radiation better than granite and sandstones. As a result they possess lower soil temperatures during the growing season and conserve water better. Such soils occur in many mountain ranges of the Great Basin and are undoubtedly an important factor in accounting for the present distribution of Population II trees. Dolomites are also poorer in nutrients than granites and sandstones and thus discourage sagebrush, one of the important competitors of the bristlecones in the White Mountains. In regions where there is more abundant water, the trees grow rapidly and are more subject to heart rot. These conditions characterize the Colorado stands of bristlecone pine and the stands of *P. balfouriana*, where great longevity does not occur.

Phylogeny

In the preceding account something of the character, habits, and present distribution of the pines of subsect. *Balfourianae* has been established. It is now desirable to enquire into their phylogeny. The geological period and region of origin of the genus *Pinus* will probably never be known precisely. However, North American pines can usefully be discussed in terms of an origin in the Mesozoic era in the general area now occupied by the Bering Sea. Mirov (1967) has given an excellent account of the paleobotany and paleogeography of the pines. The present taxonomic differentiation and geographical distribution of pines can be viewed as the product of changes, in the first instance taking place slowly over the long Tertiary period, and in the second instance occurring rapidly and in some cases dramatically as a result of large geological and climatic changes beginning in the Pliocene and continuing through the glacial activity of the Pleistocene.

Throughout the Tertiary period there was a gradual cooling which, in western North America, led to a general migration of floras to the south (Chaney, 1947). Under this climatic pressure and directed by the geological changes which were occurring and by the physiographic features encountered, the pines moved southward and differentiated. By the Eocene a fossil pine, determined by Axelrod (1966) as *Pinus crossii* Knowlton, and very similar to the present bristlecone pines, was growing in northeastern Nevada in what is now the northern Great Basin, under similar though probably less severe climatic conditions. *Pinus crossii* was named, however, on the basis of more recent fossil remains from the vicinity of Creede, Colorado (Knowlton, 1923). The fossil-bearing deposits at Creede have been dated by radiometric means at about 27 million years before present and are therefore probably of the latest Oligocene (Steven *et al.*, 1967). Figures 34–37 are photographs of fossil remains determined to be *P. crossii* from Creede selected from the collection at the Museum of the University of Colorado. A photograph of the small aborted first-year cone (Fig. 34) has been previously published and discussed by Cockerell (1934). The remaining three fossils have not, as far as known, been previously discussed. These fossils bear a very close resemblance to the contemporary trees of Population I. The cone is indistinguishable, as first pointed out by Cockerell and again verified in connection with this study, from an aborted first-year cone of a Population I tree. The bristles are much too long and stout to be confused with similar cones from the other three populations. Moreover the needle impressions of the fossils shown in Figs. 36–37 show single longitudinal lines that appear to be dorsal grooves similar to those which overlie the single resin ducts of Population I trees. The incredibly clear impression of an articulate seed wing shown in Fig. 35 is identical with contemporary seed wings. It is concluded from this evidence that pines of subsect. *Balfourianae*, essentially identical with modern trees of Population I, were growing in Colorado 27 million years ago and under conditions not very different from those where Population I trees grow today. Indeed bristlecone pines are growing today within a mile of some of the Creede fossil formations, but there is no way of knowing whether bristlecones have been present in the Creede vicinity continuously for the past 27 million years.

Geological studies have shown that the orogeny giving rise to the Rocky Mountains was far advanced 27 million years ago. With the evidence of the Creede fossils it is safe to assume that the southward migration of ancestral bristlecone pines followed at least one route far from the Pacific coastal regions. The presence of Populations III and IV in California is interpreted as indicating that the ancestral pines found another generally southward migration route far to the west of the route to Colorado. The far western route was probably followed

Figures 34–37.—Late oligocene fossils of *Pinus crossii* Knowlton from Creede, Colorado (Mineral County).—Reproduced at actual size—Fig. 34. Aborted first-year cone (U. of Colo. 19694).—35. Type, articulate seed wing (U. of Colo. 19698).—36. Five-needle fascicle (U. of Colo. no number).—37. Branch showing needle retention and many needles with traces of single grooves or ducts (U. of Colo. 18654).

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somewhat later than the route to the Rockies. The present understanding of the geological history of western North America (Hunt, 1956; 1967) does not suggest that any feasible routes of migration from the presently occupied California stations to the Rockies have ever existed for pines requiring subalpine habitats. The region of the Colorado Plateau and the Colorado-Green River system at the time of the Creede fossils was considerably lower and therefore in all probability as serious a barrier as it is today. Any attempt at a detailed discussion of the dispersal and migration processes is beyond the scope of the present investigation. Let it suffice to point out that the Owens Valley is accepted today as a sufficient barrier to pine migration and introgressive hybridization to keep Populations II and III distinct.

Turn now to the trees of Populations II, III, and IV. From their differences, taken collectively, from Population I trees, and from what is known of the fossil ancestors of Population I trees, it seems possible that their ancestors separated in their migration southward from the ancestors of Population I trees as long ago as the Paleocene or even the late Cretaceous, and from a station far to the north or northwest of any occupied by their descendants today. As a matter of pure speculation it is suggested that the trees of Population IV are probably most like the ancestral population in that they have migrated the least and occur in a habitat requiring the least selective adaptation. The disjunction between Populations III and IV probably occurred during the early Pleistocene at the time of the final uplift leading to the present configuration of the Sierra Nevada.

What then of Population II? On the basis of the similarities in needle structure, branching habits, and in chemistry, a closer relationship seems indicated with trees of Population III than with trees of Population I. The following hypothesis is offered to explain the relationship. Before the diastrophism which resulted in the present Cascade-Sierra Nevada Mountain system, it is known from abundant paleobotanical evidence that the climate in the Great Basin region was much less extreme than at present and that temperate forests, not unlike those now present on the western slopes of the Sierra Nevada, were present, for example, in regions of Nevada that are now extremely arid and that experience very cold winters (Axelrod, 1940; 1962). Fossil remnants identified as *Pinus crossii* bear witness that the ancestral bristlecone pines found suitable habitats in the uplands then existing. It may be supposed that these trees were substantially identical with the ancestors of Population III and IV, but not of Population I. Then, beginning in the Pliocene, a sometimes halting uplift began which resulted in the present Sierra Nevada. The final stages culminated in the Pleistocene, according to the fossil pollen studies of Axelrod and Ting (1960; 1961). In response to the gradual desiccation, which took place over a time span of about 5 million years, the ancestral Population II trees became restricted to mountain locations where there was enough precipitation and where edaphic conditions were suitable. Biotypic selection, it is supposed, must have been comparatively rapid for such hitherto conservative pines, and, as a consequence, a population, which has been discussed as Population II, developed. As an accompaniment of the selective adaptation to much lower precipitation, it is postulated that the trees acquired

cones with more scales and longer bristles—cones which, when ripe, more closely resemble cones of Population I than Population III trees. It is known from such work as that of Wells and Berger (1967), Critchfield and Allenbaugh (1969), and Mehringer and Ferguson (1969) that the climatic changes associated with the Pleistocene glaciations greatly altered conifer distributions in the Great Basin, and the present distribution must be examined in detail in the light of the climatic pressures and opportunities of the glacial periods.

It may be possible to test the phylogenetic hypothesis, formulated above in a highly simplified form, to account for Population II by a careful study of the now numerous collected fossil remains determined as *P. crossii*. For example the fossils may provide evidence of needles with two resin ducts for collection localities to the west of the Colorado-Green River system. Such fossils, if found, would suggest a need for taxonomic revision of *P. crossii* analogous to that which is proposed below for *P. aristata*. Cone fossils would be particularly interesting. Further pollen studies may also help and should begin with an intercomparison of pollen of living trees of Populations I, II and III. The latter two have indeed been compared (Axelrod & Ting, 1960), but the identification of pines by pollen is a very difficult subject and identifications are open to grave doubts (Leopold, 1969). Axelrod and Ting (1960), of course, had no grounds for considering that pollen from Population I trees might be distinguishable from that of Population II.

Turn now to the present stands of Population I trees, and consider the highly disjunct population of the San Francisco Peaks of Arizona. It has been known for some time that the affinities of the subalpine and alpine flora of the San Francisco Peaks are with the Rocky Mountains of Colorado and the Sangre de Cristo Mountains of New Mexico and not with the Great Basin flora (*cf.* Little, 1941). These floristic affinities have been discussed recently by Moore (1965). It will therefore probably be of no surprise that the bristlecone pines of the San Francisco Peaks belong to Population I rather than II. But when and by what route did they arrive? The Peaks themselves are early Pleistocene volcanoes, and their subalpine and alpine plant populations can hardly have been acquired earlier. Since bristlecone pines of Population I do not occur to the north of Grand Canyon nor in southwest Colorado, it is supposed that their migration route to the San Francisco Peaks must have followed the high ground that runs, with gaps, from the vicinity of Sante Fe down the Rio Grande, crossing that river, and through the high mountains of west-central New Mexico, over into the White Mountains of east-central Arizona, and along the Mogollon Rim. The contours at 2000 and 3000 m on the distribution map (Fig. 3) illustrate the nature of this route. Moreover during the Pleistocene glacial periods, there is evidence that the various vegetation zones, such as alpine and subalpine, were situated at elevations between 500 and 1200 m lower than at present (Antevs, 1954; Mehringer & Ferguson, 1969). Under such conditions there were nearly continuous habitats for Population I trees between the Sangre de Cristo Range and the present Arizona stands. Indeed it is possible that relict stands of Population I trees may yet be found in central and south-central New Mexico along the suggested migration route.

The reason for the absence of Population I bristlecones in areas with apparently suitable habitats to the west of the known distribution in Colorado and northern New Mexico may be attributed in part to the severe competition of other subalpine conifers in these areas, which receive more precipitation than the front ranges.

TAXONOMY

As has been abundantly demonstrated in the preceding account, the taxonomic organization within subsect. *Balfourianae* is unsatisfactory. No action should be considered insofar as Populations III and IV, both *P. balfouriana,* are concerned until Mastrogiuseppe's complete findings are available and can be studied. The already known chemical difference and differences in cone and seed dimensions between these two populations suggest, at most, taxonomic distinctions at the varietal or subspecific level.

The Arizona trees of Population I seem to differ in small ways from the main population, but until these differences can be studied in greater detail and with more thoroughness than has been possible up to this time, and until chemical studies can be undertaken, no taxonomic proposals concerning them are in order.

Population II has been demonstrated to differ from *P. aristata,* as described by Engelmann (1863), in several important characters such as chemistry, needle structure, and cone characteristics. In fact, except for bristle length and cone scale number, Population II is much closer to Population III than to Population I. The longstanding confusion seems to be related to considerations such as the following:

1. Botanists of this century have tended to take for granted that the taxonomy of subalpine conifers was long ago settled and have directed their attention and interest to less obvious elements of the vegetation.

2. The ripe cones of Populations I and II, especially after some weathering and/or storage in herbarium collections, often bear a close resemblance to one another.

3. The foliage of all four populations, particularly after drying and mounting on herbarium sheets, seems similar, particularly if resin exudations are disregarded and if details of resin ducts, that require use of a hand lens to be seen clearly, are overlooked.

4. There has been general acceptance, particularly by Pacific Coast botanists, that trees of Population II growing in the White Mountains of California, having cones with conspicuous bristles, are distinct at the specific rank from the nearby foxtail pines of Population III. The convenient local availability of trees producing cones with bristles has made it unnecessary for Pacific Coast botanists to give attention to specimens from the Rocky Mountains.

5. The general acceptance by Rocky Mountain botanists that their Population I trees are *P. aristata* has left them no need to go as far as the Colorado Plateau or Great Basin to collect specimens.

6. The general acceptance by botanists whose interests lie mainly in the Colorado Plateau and Great Basin regions that Population II trees, having con-

spicuous bristles, are *P. aristata* has deprived them of incentive to examine specimens from the Rocky Mountains.

It is useful at this point to re-examine Figure 3 and to recall:

1. The complete geographic separation, at present by about 250 km, between the closest stands of trees of Populations I and II, a separation that has probably existed for their respective ancestors since middle Tertiary time or earlier.

2. The probable relatively recent separation and differentiation of Population II from Population III, and the smallness of their geographical separation today, particularly with respect to the possibility of natural hybridization[10] by pollen dispersal across the Owens Valley, where the distance between them is no more than about 35 km.

The main difficulty encountered is in deciding what constitutes *Pinus aristata.* As stated earlier, Engelmann himself decided that the entire foxtail-bristlecone pine complex might better be regarded as a single species with two races. *Pinus aristata,* which for a century has been interpreted to include Populations I and II, is now shown to consist of two obviously discordant elements, one of which seems more naturally allied with *P. halfouriana, sensu stricto,* than to *P. aristata, sensu stricto.* The problem, then, is to decide the status of Population II. To make it a subspecies or variety of Population I would seem unsatisfactory in the face of the evidence submitted above. The same evidence makes a strong case for describing Population II as a subspecies or variety of Population III. The solution, then, in view of the hitherto accepted taxonomic arrangements in subsect. *Balfourianae,* with their inevitably subjective elements, is to establish Population II as a distinct species. This solution confines *Pinus aristata* Engelm., *sensu stricto,* to Population I, the most distinctly different of the four populations examined, and leaves it a good species. For the new species the following diagnosis is supplied:

Pinus longaeva D. K. Bailey, sp. nov.

Arbor pendulo-ramosa quae folia plus annos 30 retinere et in locis aridis et altissimis plus annos 4000 vigere potest. Folia stomata tantum in faciebus ventralibus habent atque duos ductus resiniferos, parietibus crassis, magnos et externos; in facie dorsali non modo sulcus (vel sulci) longitudinalis in ductus resiniferos superpositus deest, sed neque resina in globulos conspicuos et albidos exudatur. Megastrobili juveniles fusiformes, purpurei, rarenter flavo-viridi; megastrobili maturi rufescentes, basibus rotundatis vel obtuso-conoideis et axibus non curvatis; squamae circiter 120; umbones dorsales in aristas tenues extenti quae strobilis maturis saepe recurvantur.

UNITED STATES. NEVADA: White Pine County, Wheeler Peak Scenic Area, Humboldt National Forest, 39° 00′ N, 114° 18′ W, elevation 3200 m, substrate coarse quartzite boulders, 20 June 1970, *D. K. Bailey & J. E. Whitson 7001.* Holotype, COLO; isotypes, ARIZ, BRY, CAS, E, GH, HSC, K, LE, MO, NA, NY, RENO, RM, S, TI, UC, UNM, US, USFS, UT, UTC, W, and the Institute of Forest Genetics, U. S. Department of Agriculture, Placerville, California.

---

[10]Successful hybrids between Population II and III are growing at the Institute of Forest Genetics, Placerville, California. Hybridization experiments between Population I and both Populations II and III have not, as far as is known, yet been attempted.

Figure 23 shows a needle cross section from the type specimen.

The distinguishing characters of the new species, the most remarkable of which is its extraordinary longevity, taken note of in the specific epithet, have already been discussed. To have made all populations of subsect. *Balfourianae* into a single coenospecies with distinct varieties or subspecies would probably have done taxonomic injustice to *P. aristata, sensu stricto,* particularly when the taxonomic distinctions among other closely related pine species are considered in comparison.

The new species proposed above necessitates some revision in the common names. Population I trees, *P. aristata,* should probably be described, when there is a need to be explicit, as "Rocky Mountain" bristlecone pines. Then under similar circumstances the Population II trees, *P. longaeva,* could be referred to as "Great Basin" bristlecone pines, though in view of their greater needle retention and closer relationship with Population III trees, "Great Basin" foxtail pines might be preferable.

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Appendix I

Distribution of specimens by populations

HERBARIA VISITED—Distribution based on examination of specimens.	POPULATION I	II	III	IV	TOTAL
University of California, Berkeley (UC)	10	38	15	8	71
New York Botanical Garden (NY)	23	27	5	8	63
Missouri Botanical Garden (MO)	20	20	6	4	50
University of Colorado (COLO)	23	10	9	8	50
U. S. National Herbarium (US)	23	16	3	3	45
Institute of Forest Genetics, Placerville, California	5	14	8	11	38
Intermountain Herbarium, Utah State University, (UTC)	1	29	2	0	32
Rocky Mountain Herbarium, University of Wyoming (RM)	8	10	6	0	24
Brigham Young University, Provo, Utah (BRY)	3	16	0	0	19
University of Utah (UT)	1	17	1	0	19
University of Nevada (RENO)	1	15	0	0	16
National Arboretum, Washington, D.C. (NA)	5	10	0	0	15
University of New Mexico (UNM)	14	0	1	0	15
U. S. Forest Service, Washington, D.C. (USFS)	1	11	1	1	14
University of Arizona (ARIZ)	12	0	0	0	12
Colorado State University (CS)	11	0	0	0	11
Jepson Herbarium, Berkeley, California (JEPS)	0	3	5	2	10
TOTALS	161	236	62	45	504
HERBARIA NOT VISITED—Distribution based on lists with collection information supplied by curators.					
Dudley Herbarium, Stanford University, Palo Alto (D S)	8	23	21	9	61
California Academy of Sciences (CAS)	5	15	23	8	51
Arnold Arboretum, Jamaica Plain, Mass. (AAH)	18	14	8	4	44
Gray Herbarium, Harvard University, Cambridge (GH)	7	12	5	2	26
TOTALS	38	64	57	23	182
FRESH SPECIMENS EXAMINED—Collected by or for the author.	39	37	14	7	97

Appendix II

VARIATION WITHIN GEOGRAPHICAL GROUPINGS OF FIGURE 8

Population	Locality	Needles With at Least One Resin Exudation — Number of such needles per fascicle							Needles With a Single Resin Duct in the Distal Quarter — Number of such needles per fascicle						
		5	4	3	2	1	0	Total	5	4	3	2	1	0	Total
I	Colorado: North of Arkansas River	83	14	3	—	—	—	480	69	26	4	1	—	—	463
I	Colorado: South of Arkansas River and New Mexico	76	15	5	2	2	—	461	47	26	17	10	—	—	410
I	Arizona: Mt. Agassiz (first half of sample)	28	26	13	11	15	7	320	41	33	20	3	2	1	405
I	Arizona: Mt. Agassiz (second half of sample)	13	23	33	17	11	3	301	54	32	11	3	—	—	437
II	Utah and Nevada	—	—	1	7	18	74	35	—	—	—	1	5	94	7
II	California: White Mountains	—	—	—	3	11	86	17	—	—	—	1	15	84	17
III	California: Sierra Nevada	—	—	1	4	24	71	35	—	—	—	—	3	97	3
IV	California: Klamath Mountains	—	—	2	5	19	74	35	—	—	—	—	6	94	6

Appendix III

NEEDLE VARIABILITY IN POPULATION I USING 40-FASCICLE (200-NEEDLE) SAMPLES

	Mt. Evans Colorado	Mt. Evans Colorado	North Pass Colorado	Creede Colorado	Mt. Agassiz Arizona	Mt. Agassiz Arizona
Needles with single resin duct for entire length						
Total number	121	163	128	69	74	34
Number with no resin exudations	0	3	38	4	31	28
Total number of resin exudations	190	254	109	91	48	6
Needles with a variable number of resin ducts but with a single duct along the distal quarter length						
Total number	60	10	11	87	100	126
Number with no resin exudations	0	0	4	5	20	96
Total number of proximal resin exudations	38	11	4	114	28	4
Total numer of distal resin exudations	80	11	4	55	90	28
All needles terminating with a single duct along the distal quarter length						
Total number	181	173	139	156	174	160
Total number of resin exudations	308	276	117	260	166	38
Needles with two resin ducts for entire length						
Total number	19	27	61	44	26	40
Number with no resin exudations	0	0	11	0	8	29
Total number of resin exudations	45	59	83	103	23	12
Total number of needles having at least one resin exudation (200 minus number of needles having no resin exudations)	200	197	147	191	141	47
Total number of resin exudations in entire 200-needle sample	353	335	200	363	189	50

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NOTES

STUDIES IN *SOLIDAGO*. I. THE *SOLIDAGO GRAMINIFOLIA-S. GYMNOSPERMOIDES* COMPLEX

Attempts to delimit *Solidago gymnospermoides* (Greene) Fern. as a specific entity from *S. graminifolia* (L.) Salisb. var. *media* (Greene) Harris have proven unsuccessful. Although *S. gymnospermoides* differs from the typical variety of *S. graminifolia,* it is not specifically distinct from var. *media* which in turn is not specifically distinct from the typical variety. Numerous intermediate plants are found between *S. gymnospermoides* and *S. graminifolia* var. *media,* and they are frequently morphologically indistinct where their ranges merge. The following change is therefore proposed:

Solidago graminifolia var. *gymnospermoides* (Greene) T. B. Croat, *comb. nov.*
Euthamia gymnospermoides Greene, Pittonia 5: 75. 1902.
Solidago gymnospermoides (Greene) Fern., Rhodora 10: 93. 1908.

Solidago graminifolia var. *media* is characterized by branching well above the middle. It has glomerulate, somewhat glutinous, turbinate heads, and weakly punctate leaves with distinct veins. On the other hand, var. *gymnospermoides* branches below the middle and has pedunculate, strongly glutinous, cylindrical heads. Its leaves are strongly punctate and narrow with indistinct veins. Both taxa vary as much locally as they do throughout their ranges.

An analysis was carried out on plants of var. *media* and var. *gymnospermoides* making use of all key characters (Table 1). Specimens were studied throughout the range of both taxa with the majority from Kansas, Nebraska, Iowa, and Missouri. The two taxa are sympatric throughout most of their ranges—var. *gymnospermoides* ranges from Colorado to northwestern Texas, east to Wisconsin, Illinois and Arkansas; while the var. *media* ranges from Minnesota to Kansas, east to Wisconsin and Ohio.

Numerous intermediate plants were found, *i.e.* those appearing to belong to one taxon but having characters in common with the other. In a total of 141 plants, 47 (33%) were definitely intermediate between the two varieties and exhibited from two to three characters attributed to the other.

Intermediate plants of var. *gymnospermoides* (KANSAS. ELLSWORTH CO.: *Wagenknecht 2336;* SHAWNEE CO.: *Volle 846,* both KANU) differ from the typical var. *gymnospermoides* by having branches above the middle, less glutinous phyllaries, wider and more frequently glomerulate heads, and more distinctly veined and less punctate leaves. Intermediate plants of var. *media* (KANSAS. ROOKS CO.: *Imler 4873;* SHERIDAN CO.: *McGregor 15222,* both KANU) differ from typical plants of var. *media* by branching lower on the stem, having longer, more glutinous involucral bracts, more definitely pedunculate heads and leaves with less distinct venation and more obvious punctation.

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TABLE 1: Character analysis of *S. graminifolia* var. *media* and var. *gymnospermoides*. Where appropriate, minimum, mean (*italicized*), and maximum measurements are given.

Character	Typical var. *gymnospermoides*	Intermediate var. *gymnospermoides*	Intermediate var. *media*	Typical var. *media*
Number of plants studied	43	29	18	51
Length of involucre (mm)	4.0–*5.54*–6.5	4.0–*5.52*–6.0	4.0–*5.54*–6.3	3.5–*4.78*–6.0
Number of rays	8–*11.88*–16	8–*11.78*–16	6–*11.84*–13	6–*11.32*–18
Number of disks	3–*5.56*–9	3–*5.09*–7	3–*4.87*–7	3–*4.65*–9
Width of leaf (mm)	1.5–*3.15*–5.3	2.4–*5.09*–7.0	3.2–*5.28*–10.0	2.5–*4.90*–8.3
Leaf venation				
Very distinct	2%	11%	35%	56%
Weakly distinct	36%	34%	53%	38%
Not obvious	62%	55%	12%	6%
Involucre				
Very glutinous	62%	59%	41%	14%
Weakly glutinous	33%	28%	35%	35%
Not glutinous	5%	13%	24%	51%
Leaf punctation				
Strong	78%	75%	61%	14%
Weak	22%	25%	17%	26%
Absent	0%	0%	22%	60%
Inflorescence branching				
Above middle	36%	88%	88%	97%
At middle	10%	6%	6%	3%
Below middle	54%	6%	6%	0%
Glomerulation				
Nearly all heads glomerulate	2%	7%	11%	80%
Most heads glomerulate many pendunculate	10%	25%	22%	7%
Equal numbers of heads glomerulate and pedunculate	12%	7%	6%	6%
Most heads pedunculate many glomerulate	33%	32%	39%	7%
Nearly all heads pedunculate	43%	29%	22%	0%

On the basis of this investigation, it appears that the two taxa are very closely related and that they are merely intraspecifically distinct. The mean number of ray and disk flowers for the two taxa are very close, approximately 11 rays and 5 disks for each species. The other varieties of *S. graminifolia* have many more florets, averaging 25 rays and 13 disks for var. *graminifolia* and 21 rays and 7 disks for var. *major*.—*Thomas B. Croat, Department of Biology, Washington University and Missouri Botanical Garden.*

THE GENUS *CYMBOSEMA* (LEGUMINOSAE): NOTES AND DISTRIBUTION

Cymbosema is a monotypic genus containing the species *C. roseum* Benth. The genus was placed in the tribe Phaseoleae by Bentham and Hooker (Gen. Pl. 1:534. 1865). *Cymbosema roseum* is a papilionaceous legume.

During the course of my studies in *Dioclea,* a genus which also falls within the tribe Phaseoleae, it became apparent that *Cymbosema,* outside of its familiar tropical South American distribution, was being confused with *Dioclea guianensis* Bentham.

Cymbosema roseum was described by Bentham (Hook. Jour. Bot. 2: 60. 1840). The species was described and illustrated in Bentham's treatment of the legumes in Martius' *Flora Brasiliensis* (15(1):160. 1859). In this work Bentham placed the binomial *"Dioclea purpurea* Pöpp. et Endl., Nov. Gen. et Sp. III. 59. *ex descript."* in the synonymy of *Cymbosema roseum.* This seems to indicate that Bentham did not see the Poeppig type specimen, although a Poeppig specimen, "ad confluentiam fluminum Teffé et Amazonum," was cited (Martius, *loc. cit.*). This is the type locality of *D. purpurea.* Perhaps Bentham felt that the specimen did not match Poeppig's description.

I examined a specimen, apparently collected by Poeppig, from the type locality of *Dioclea purpurea—Poeppig? D 2619* (W). In agreement with Bentham, I found the specimen to be equivalent to *Cymbosema roseum.*

Philipp Salzmann collected in the state of Bahia in Brazil (Urban *in* Fl. Bras. 1(1):100. 1906), and several of his specimens have been determined as new species of *Dioclea.* None of the specimens which I have examined belongs to the genus *Dioclea,* and none of these names, to my knowledge, has been validly published. Unfortunately several types and type photographs of "*D. purpurea ined.* Salzmann" have been distributed. These specimens should not be confused with the legitimate binomial *D. purpurea* Poeppig & Endlicher. The specimens determined "*D. purpurea* Salz." represent *Calopogonium mucunoides* Desv. and are cited by Bentham (Fl. Bras. 15(1):140. 1859) under *Stenolobium brachycarpum.*

In 1944 Pittier transferred *Dioclea apurensis* HBK. (Nov. Gen. Sp. 6: 438. 1824) to *Cymbosema* and made the new combination *C. apurense* (H.B.K.) Pittier (Min. Agric. Cría, Bol. Tecn. 5:69. 1944). A figure of the perianth dissection was also published (Pittier, *loc. cit.,* Fig. 30). Following the text a list of Venezuelan collectors up to 1942 is given, and "*Humboldt, A. von, & Bonpland, A. s.n.*" is the only collection listed with the *Cymbosema apurense* determination (Pittier, *op. cit.,* p. 158). The HBK type specimen at P (not seen) and type photo (US) show vegetative and fruiting material only.

Pittier's floral description, and perianth dissection probably came from two Orinoco specimens, *Rusby & Squires 202* (GH) and *Rusby 202* (US). A note affixed to the US specimen apparently by Killip indicates the specimen was collected at the type locality of *D. apurensis,* the junction of the Apure and Orinoco Rivers in Venezuela. Killip compared the US specimen with NY material

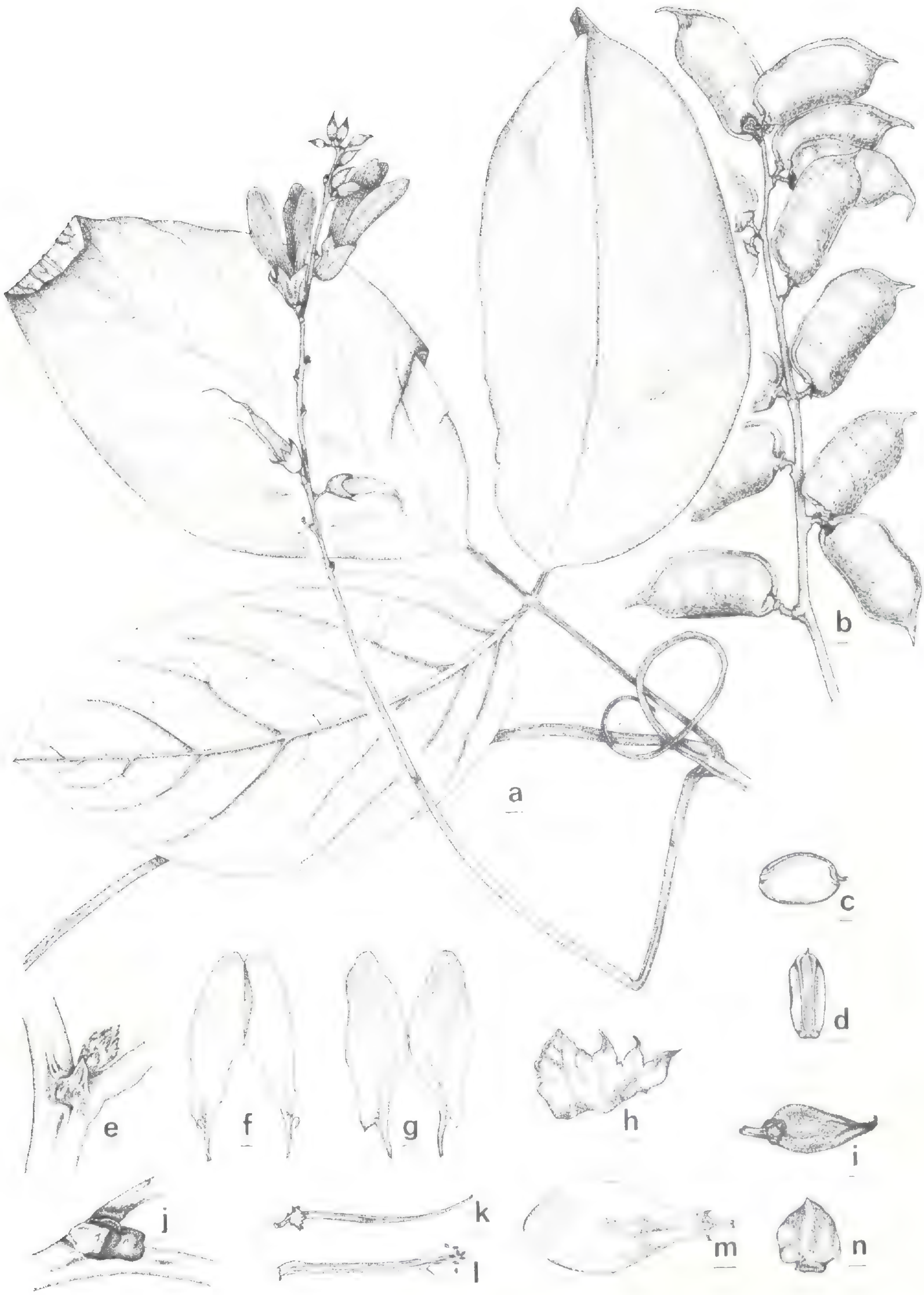

FIGURE 1. *Cymbosema roseum*.—a. Habit, × ½.—b. Mature fruits, spread on rachis, exaggerated × ½.—c. Seed, lateral view, × 1.—d. Hilum of seed, × 1.—e. Stipule, × 1.—f. Keel petals, × ⅚.—g. Wing petals, × ⅚.—h. Calyx, external view, × ⅚.—i. Bud, × 1½.—j. Bract, × 4.—k. Gynoecium, × ⅚.—l. Androecium, × ⅚.—m. Standard, × ⅚.—n. Bracteole, × 1½. [Original drawing by Mr. Craig Seliger.]

and, although there were discrepancies, placed the sheet under *D. apurensis*. Both specimens lack fruiting stages. The US specimen is annotated *Cymbosema apurense* by H. Pittier, March 5, 1941. Pittier's Fig. 30, details of the flower (Pittier, *op. cit.*, p. 69), seems to have been taken from an immature flower dissection in the smaller packet affixed to the US specimen. I have annotated both sheets *C. roseum*.

Amshoff, in 1939 (Meded. Bot. Mus. Herb. Rijks. Univ. Utrecht 52: 70), emended the description of *D. apurensis* to include floral characteristics. She compared the fruits from the type (P, not seen) to those of a Suriname specimen, *Versteeg 797* (U), which also has flowers, and compared the flowers of *Versteeg 797* to flowers of *Chaffanjon 916* (P, not seen) from the Orinoco River region. I have followed Amshoff, since it is certain she has examined the actual type material in P. It also seems certain that the type of *Dioclea apurensis, Versteeg 797*, and *Chaffanjon 916* are within the limits of the genus *Dioclea* rather than *Cymbosema*. I reject Pittier's transfer of *Dioclea apurensis*, based on a study of the type photo, the original description, and the misidentification of the Rusby and Squires specimens.

The main diagnostic characters of *Cymbosema* are the falcate, ca. 4-seeded fruit, usually with a long, downcurved persistent style, the free vexillary stamen, the flower length and reddish color, and the extension of the lower calyx lobe forming an apiculate tip in the bud. Flower color is not entirely reliable. The color of *Cymbosema* apparently changes from reddish to shades of purple upon drying. The characters which separate *Dioclea* section *Dioclea* Benth. from *Cymbosema* are the fused vexillary stamen, the blue to reddish-purple flower color, and the narrowly oblong fruit with 6–12 seeds. The two species of *Dioclea* with the longest flowers, *D. fimbriata* and *D. macrantha* (both with flowers ca. 4.5 cm long), share the geographic range with *Cymbosema* and also may share the non-reflexed standard petal character. The fruits should not be confused—the seed number of the two species of *Dioclea* is ca. 10.

The separation of *Camptosema* Hook & Arn. from *Cymbosema* is more difficult and depends primarily on the fruits. Some species of *Camptosema* have the vexillary stamen fused or can be separated on their flower color or extremely long calyx tube length. *Camptosema* is currently being studied by A. Burkart (personal communication).

Cymbosema roseum Benth., Hook. Jour. Bot. 2: 60. 1–2. 1840. (K, holotype; BM, F, K, US, W, isotypes. Brazil: Roraima (Rio Branco), *Schomburgk 850.*)

Dioclea purpurea Poeppig & Endlicher, Nov. Gen. Sp. Pl. 3: 59. 1845. (W, holotype? Brazil: Confluence of Tefé and Solimões (Amazonas) Rivers, *Poeppig D 2619.*)

Vine, to ca. 10 m long, semiligneous, the stems twining, terete, canescent-strigulose, becoming glabrescent. *Leaves* trifoliolate, with leaflets broadly lanceolate to oblong, stipitate, to ca. 17 cm long and ca. 11 cm wide, the margins entire, stipellate, the apex acute, sparsely strigose above, appressed-pubescent below, chartaceous, slightly cordate to truncate-rounded at the base, the laterals slightly oblique, primary lateral veins ca. 5 pairs, prominent beneath; petioles canaliculate,

strigulose, the rachis 4–20 mm long, the stipels ca. 3 mm long; stipules triangulate, ca. 3 mm long. *Inflorescences* axillary, erect, slender, 16–30 cm long, with flowers along the distal ¼–⅕ of the peduncle, the tubercles sessile; bracts ovate, ca. 1.5 mm long, persistent; bracteoles triangulate, ca. 8 mm long, puberulent without, canescent appressed-pubescent within. *Flowers* red, papilionaceous, ca. 4 cm long; the calyx campanulate, with 4 lobes, the upper lobe obtuse, ca. 4 mm long, the laterals acute, ca. 4 mm long, the lower lanceolate, ca. 5 mm long; lamina of the standard obovate, membraneous, puberulent, ecallose, to ca. 40 mm long and ca. 20 mm wide, basally biauriculate, the auricles semi-orbicular, reflexed, the claw ca. 4 mm long; lamina of the wings oblanceolate, free, auriculate, ca. 32 mm long and ca. 7 mm wide, the claw ca. 6 mm long; lamina of the keel oblanceolate, ca. 32 mm long and ca. 7 mm wide, fused ca. 9 mm distally, auriculate, the claw ca. 7 mm long; stamens 10, diadelphous, the vexillary free, the remainder fused basally and free distally ca. 10 mm; ovary ca. 14 mm long, sessile, canescent-tomentose, ca. 6-ovulate, the stigma and style glabrous. *Fruits* oblong, ca. 44 mm long, ca. 18 mm wide, and 4 mm thick, dehiscent, canescent turning ferrugineous, finally glabrescent, falcate, frequently with a persistent style ca. 15 mm long. *Seeds* ca. 4, ca. 10 mm long, ca. 6 mm wide, and ca. 4 mm thick, hard, dark brown, lustrous, the hilum encircling nearly ½ the testa.

BRAZIL. AMAPA: Rio Urucauá, 3°36′N, 51°19′W, *Irwin 48785* (LE, U, US). AMAZONAS: São Paulo de Olivença, 24-5-1940, *Ducke* 559 (F, MO, UC, US). Rio Purus, *Huber 4645* (RB, US). Near mouth Rio Envira (Embira), 7 30′S, 70 15′W, *Krukoff 4534* (A, G, U). Fonte Boa, *Kuhlmann 1583* (RB), *Kuhlmann* RB No. *18218* (U). Confluence of Tefé & Solimões (Amazonas) Rivers, *Poeppig D 2619* (W). Near Barra, Rio Negro, *Spruce 1635* (BM, M, W). MARANHAO: Rio Pindaré, vicinity of Monção, *Fróes 20332* (US). PARA: Serra do Cachimbo, *M. Alvarenga* RB No. *90555* (RB). Boa Vista, Tapajós River, *Dahlgren & Sella 53* (F, US). Oriximiná, 15-9-1910, *Ducke 10989* (RB). Planalto de Santarém, *Fróes 31541* (IAN). Maicura, Canal Maroja neto, *Pires & Silva 4302* (NY). RORAIMA (RIO BRANCO): Without locality, *Schomburgk 850* (BM, F, K, US, W).

COLOMBIA. AMAZONAS: Amazon R. watershed, Loreto Yuca R., *Black & Schultes 46-277* (US), *Schultes 7160* (US). Between the Loreto Yacu & Hamaca Yacu Rivers, *DuQue-Jaramillo 2053, DuQue-Jaramillo 2090A* (both COL). Near mouth of Río Loreto Yuca & Puerto Nariño, *Schultes et al. 24151* (US). ATLANTICO: Barranquilla and vicinity, *Bro. Elias 369, 525* (both US), *1244, 1298* (both F, US). Barranquilla, *Bro. Paul C-22* (US). CHOCO: Río Atrato, 2–5 hours below Río Sucio, *Duke 11013* (US). Río Cacarica, *Castañeda 6335* (COL). BOYACA(?): Los Llanos region, Río Meta, Cano Avispa, *Cuatrecasas 3782* (F). Río Meta, Matacormena, *Cuatrecasas 4299* (F, US). MAGDALENA: Gamarra, *Uribe 2646* (US).

COSTA RICA. ALAJUELA: Vicinity of Los Chiles, 11°02′N, 84°44′W, *Holm & Iltis 644* (A, MO, U).

MEXICO. CHIAPAS: Las Garzas, Acapet, *Matuda 2803* (A, F, MO, NY).

PANAMA. CANAL ZONE: Barro Colorado Island, *Aviles 19b* (F), *Croat 8304* (MO), *Shattuck 255, Shattuck 1094* (both F), *Wilson 128* (F), *Woodworth & Vestal 687* (A, F).

PERU. LORETO: *Iquitos*, innundation belt of Río Itaya, *Aspund 14305* (S). Near Iquitos, *Klug 912, 1364* (both F, US). District of Iquitos, Rancho Indiana, *Mexia 6419* (BM, F, G, GH, MO, S, UC, US). Gamitanacocha, Río Mazan, *Schunke 34* (A, F, UC, US). Ucayali River region from 10 S to the mouth, *Tessmann 3370* (G). Lower Río Nanay, *Ll. Williams 530* (F, US), *667* (F). La Victoria, Amazon River, *Ll. Williams 2781* (F). Río Itaya, *Ll. Williams 8116* (F). Pucallpa, Shores of Ucayali River, *Woytkowski 6277* (MO, SIU).

VENEZUELA. AMAZONAS: Right bank of Orinoco River, opposite mouth of Río Atabapo, *Wurdack & Adderley 43742* (US, VEN). APURE: Orinoco River and vicinity of mouth of the Apure River, *Rusby 202* (US), *Rusby & Squires 202* (GH). BOLIVAR: Narosi-

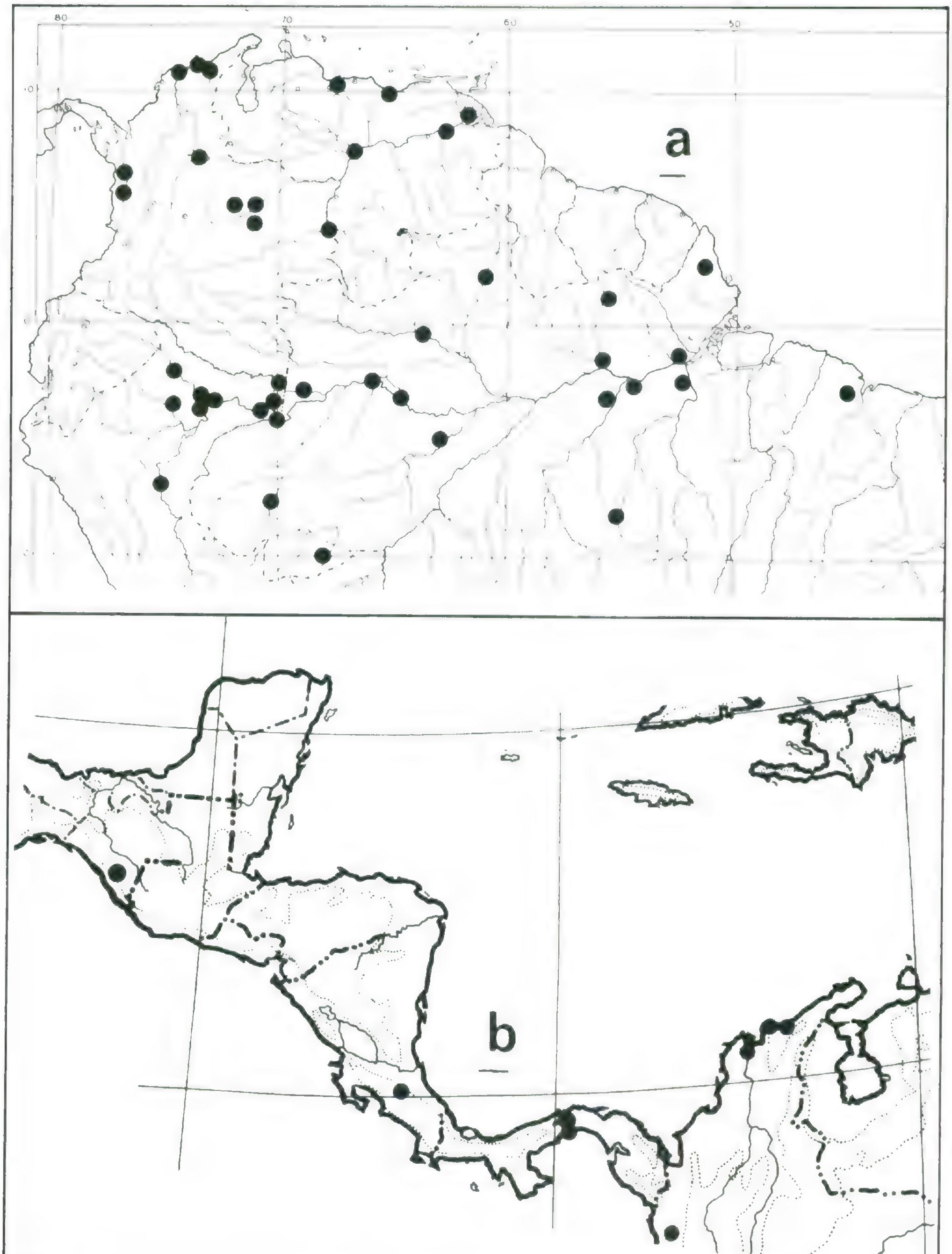

FIGURE 2. The distribution of *Cymbosema roseum*.—a. South American distribution. —b. Central American and Mexican distribution.

Tiquisio Trail (?), Land of Loba, *Curran 154* (GH, US). DELTA AMACURO: Vicinity of Tucupita, *Aristeguieta 4066* (VEN). MIRANDA: Río Chico, *Aristeguieta 2725* (VEN). YARACUY: Río Taria, between Pto. Cabello & San Felipe, *Pittier 8400* (GH, US).

To my knowledge, this is the first report of *C. roseum* occurring in Panama and Mexico. The species is probably distributed throughout the moist lowlands of Central America.—*Richard H. Maxwell, Missouri Botanical Garden* and *Department of Natural Science, Indiana University Southeast, Jeffersonville.*

A NEW COMBINATION IN *PILOTRICHIDIUM* BESCH. (MUSCI)

While compiling a list of the mosses reported for Trinidad (Crosby, Ann. Missouri Bot. Gard. 57: 145–151. 1970), I came across the name *Hookeria diatomophila* C. Müll. This species is based on a collection by Charles Wright. Müller (Hedwigia 37: 247. 1898) originally cited it as "Habitatio. Insula Trinidad Antillarum, ad rupes irroratas montium: Charles Wright in Coll. Musc. Cubens. III. No. 71. Hb. Sullivantis." Knowing that Wright did not collect on Trinidad made me suspicious of this record. However, I soon noted that later in the same paper Müller (*op. cit.*, p. 266) corrected his original citation: "Pro 'Insula Trinidad Antillarum' (p. 247) lege Cuba prope Trinidad." The city of Trinidad is on the southern coast of central Cuba.

Fleischer (Hedwigia 63: 216. 1922) transferred this species to *Callicostella* after studying the material in Müller's herbarium (B). With the destruction of this hebarium, the holotype was apparently lost. However, there is a duplicate in the Sullivant hebarium (FH). Although Sullivant (Proc. Amer. Acad. Arts 5: 273–290. 1861) published an extensive list of Wright's Cuban mosses, this collection was not included. Wright apparently collected this moss on one of his later trips to Cuba.

The specimen in FH was labeled "Cub. III. 71. Hookeria" by Sullivant. The typewritten label which has been added to the packet bears the additional information "on rocks in mountain rivulets, Güinía, Trinidad. March 4, 1867." "Güinía" is probably Güinía de Miranda, located about 30 km NNE of Trinidad. An annotation by H. A. Crum identifies the moss as *Pilotrichidium leonii* (Thér.) Crum & Bartr. Examination of several syntypes of *P. leonii* confirms this. However, the epithet *diatomophila* antedates *leonii* and must be used for this species.

Pilotrichidium diatomophilum (C. Müll.) M. R. Crosby, *comb. nov.*

Hookeria diatomophila C. Müll., Hedwigia 37: 247. 1898. [CUBA. Güinía, Trinidad. Wright, Cub. III. No. 71 (FH, lectotype).]

Callicostella diatomophila (C. Müll.) Fleisch., Hedwigia 63: 216. 1922.

Callicostella leonii Thér., Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 14: 367. 1940. [CUBA. Sierra de banao, *Léon & Clément 5473, 5502, 8251*

(all NY, syntypes). Bayate de Miranda, *Ekman 2615* (NY, syntype). Pan de Guajaibon, *Acuña 531* (syntype, not seen).]

Pilotrichidium leonii (Thér.) Crum & Bartr., Bull. Inst. Jamaica, Sci. Ser. 8: 48. 1958.

I thank Winona H. Welch, DePauw University, for pointing out the existence of the Wright collection and the curators of FH and NY for the loan of specimens.
—*Marshall R. Crosby, Missouri Botanical Garden.*

SOLANACEAE STUDIES. I

1. SOLANUM CAROLINENSE var. FLORIDANUM

Solanum carolinense L. var. *floridanum* Chapm., Fl. S. United States Ed. 1. 349. 1860, "floridana." Type: "In apricis prope St. Marks Florida" May 1843, *Rugel s.n.* (G-DC not seen, photos MO, US; MO, NY).

Solanum floridanum Shuttlw. *ex* Dun. *in* DC., Prodr. 13(1): 306. 1852 non Raf., Aut. Bot. 107. 1840.

Solanum godfreyi Shinners, Sida 1: 108. 1962.

A first glance might suggest that the varietal name *floridanum* is incorrect because *S. floridanum* Dun. is a later homonym. However, under Article 72 of the 1966 *Code* Chapman must be considered to have published a new and valid epithet rather than a transfer of Dunal's illegitimate epithet.

This variety is distinguished from the typical by the very deep lobing of its leaves. It is restricted to north Florida and perhaps neighboring Georgia and is most commonly found between the Suwannee and Apalachicola Rivers and along the St. Johns River. It is found in habitats much like those of the typical variety with perhaps a tendency to grow in slightly moister sites. Mauve, blue and white flowered forms sometimes occur together. Chromosome number n = 12 [*D'Arcy 3501* (seed of *D'Arcy 1212A*) (FLAS)].

A herbarium sheet of typical var. *floridanum* material may give one full confidence that this is a distinct species. However, in the field all intermediates with typical *S. carolinense* are found (Fig. 1), usually within a few feet of one another. Its local occurrence and distinctive leaf shape demand taxonomic recognition, but the apparent floral identity with var. *carolinense* and the occurrence of intermediates with the latter place recognition at the varietal level.

Representative specimens seen (all from Florida): CLAY CO.: W side of Doctor's Inlet, D'Arcy *1212A* (FLAS). DUVAL CO.: South Jacksonville, 1897, *Churchill* s.n. (MO); waste ground (*sine loco*), *Fredholm 5211* (GH). FLAGLER CO.: Haw Creek near Deanville, 1942, *West s.n.* (FLAS). FRANKLIN CO.: Apalachicola, *Chapman s.n.* (MO). HERNANDO CO.: Brooksville, 1938, *Phillips, Woodbury & Bushnell s.n.* (BUS). LEVY CO.: Near Wekiva River, Gulf Hammock, 1937, *West & Arnold s.n.* (DUKE, FLAS). PUTNAM CO.: Canal bank E of East Palatka, 1940, *West & Arnold s.n.* (FLAS). ST. JOHNS CO.: Roadsides and waste places, 1877, *Reynolds s.n.* (MO). TAYLOR CO.: Clearings of swampy woodland, vicinity

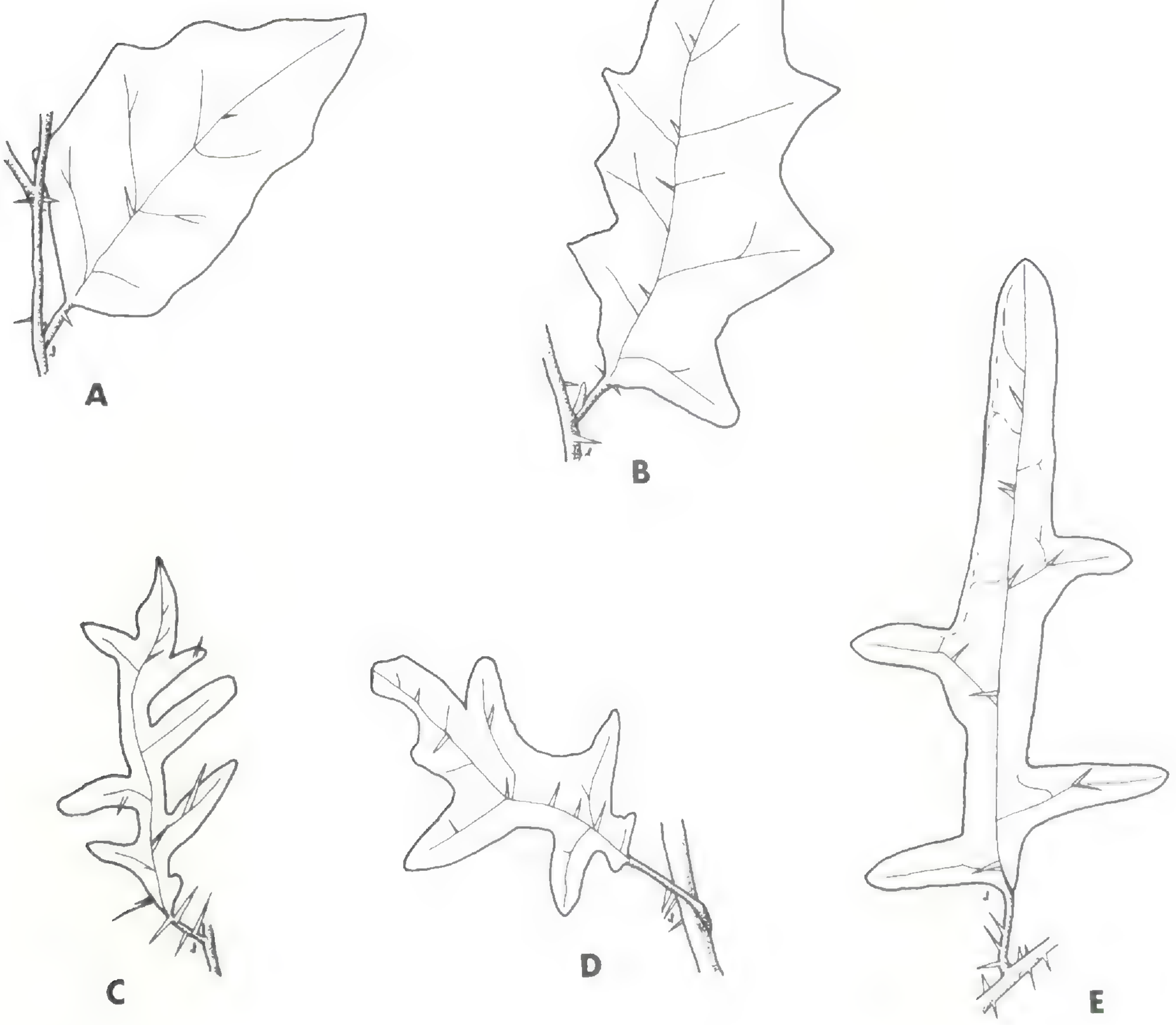

FIGURE 1. Some leaf shapes in *Solanum carolinense* (× ⅔).—A B. Variety *carolinense*.—C–E. Variety *floridanum*. [A, after *Brinker 17* (MO), roadside in Pensacola, Florida; B, after *Curtiss 4400* (MO), near Jacksonville, Florida; C, after *Rugel s.n.* (MO); D, after *Churchill s.n.* (MO); E, after *Reynolds s.n.* (MO).]

of Nuttal's Rise, along Aucilla River, *Godfrey 60037* (FSU, SMU); along roadside near low hammock, Aucilla Wildlife Management Area, *McDaniel 4297* (FSU, UNC). WAKULLA CO.: Moist clearing of deciduous woodland, Wakulla, *Godfrey 56815* (FSU, GH, SMU).

2. BRUNFELSIA DWYERI

Brunfelsia dwyeri D'Arcy, sp. nov.

Frutex v. arbor tenuis ad 10 m alta, glaber, vix foliosus, cortice cinerascenti fisso et desquamato tecti, virgulis ut videtur interdum angulatas vel complanatas. Folia coriacea glabra, elliptica v. oblanceolata, plerumque 4–10 cm longa, 1.5–4.5 cm lata, apice acuminato, basi acuto, margine integro, lamina sursum e nervio medio leviter flexa, nervis lateralibus obsoletis (prominentibus in sicco);

petiolis superne canaliculatis, plerumque brevibus, 3 (raro 12) mm longis. Inflorescentiae ex floribus singulis, axillaribus fere terminalibus consistens; pedunculus ad 6 mm longus, saepe (praesertim in fructu) obsolescens, bracteas squammosas una pluresve instructus. Pedicelli glabri, 5–15 mm longi, sursum leviter dilatati. Calyx primulinus, ellipsoideus, in sicco tubularis ut videtur, ca. 15 mm longus, saepe plane striato-verrucosus propter tubercula suberosa, coriaceus crescens; calyx in fructu aliquot accrescens et suturam unam pluresve findens. Corolla speciossissima, hypocraterformis, ostrina albescens dum deflorescens, ocellum parvum luteum habens; tubo 3–4 cm longo, 3–4 mm lato, vix arcuato; limbo 3–4 cm diametro plus quinque lobos orbicularos 2.5 cm longos instructo. Stamina inclusi. Acinus coriaceus, atro-olivaceus, plerumque tuberculatus, ovoideus, 1.5–2.5 cm per transversum, apice unum duove sulcos cruciatim obsito. Semina ca. 20 in loculis duobus contenta, testam mollem crassam translucidam obtecta, in sicco porphyrea, prismatica, 9 mm longa.

Nomen Johnanni D. Dwyeri profesoris collectoris plantarum panamensium designatur ad hanc *Brunfelsiam*. Differt haec species a *Brunfelsia* panamensi altera, floribus ostrinis albescens non lutescens, tubo breviore et limbo latiore.

Slender, glabrous *tree* to 10 m tall; bark grey-white, flaking; twigs often appearing angled or flattened. *Foliage* rather open; leaves coriaceous, elliptic to slightly oblanceolate, mostly 4–10 cm long, 1.5–4.5 cm broad, acuminate at the apex, acute at the base with entire margins, the lamina upfolded from the somewhat recurved midrib; petioles mostly short, 3 (rarely 12) mm long, channeled above. *Inflorescence* of solitary, axillary, almost terminal flowers; the peduncle to 6 mm long, often (especially in fruit) almost absent, bearing several scale-like bracts; pedicels glabrous, 5–15 mm long, broadening gradually upwards. *Calyx* yellow, ellipsoidal, appearing tubular when dried, ca. 15 mm long, often conspicuously striate-verrucose with corky excrecences, coriaceous; the lobes obtuse, ca. 4 mm long, converging on the corolla tube; the entire calyx enlarging somewhat and splitting at one or more sinuses in fruit. *Corolla* very showy, deep purple fading to white before falling but maintaining a small yellow eye; tube 3–4 cm long, 3–4 mm broad, slightly curved, the limb salverform, 3–4 cm across plus the five 2.5 cm long orbicular lobes. *Stamens* included. *Fruit* a leathery, dark greenish-brown, globose-ovoid berry, usually warty, 1.5–2.5 cm across, the apex usually crossed by a pair of sutures. *Seeds* in two locules, many, with a soft thick translucent testa which drys reddish brown, prismatic, 9 mm long.

TYPE: "Cerro Jefe in *'Cleusia'* [*sic*] forest at 2700–3000'. Shrub, flowers purple to whitish purple, Prov. Panama," *Tyson, Dwyer & Blum 3312* (MO-1820936, holotype; MO, isotype).

This very attractive small tree will make a fine addition to tropical gardens, if it can be brought into cultivation and propigated regularly. The large showy flowers sometimes appear in many shades from deep purple to white at the same time, and they are thus reminiscent of *Solanum wrightii* Benth. which is cultivated as a street tree in India and appears from time to time in the Florida nursery trade.

FIGURE 2. *Brunfelsia dwyeri* D'Arcy (× ½). [After *Correa & Dressler 471* (MO).]

Superficially, *Brunfelsia dwyeri* resembles *B. lactea* Krug & Urb. from the Luquillo Mountains of Puerto Rico, but it has a shorter tube and the flowers of *B. lactea* are greenish or yellowish white. Probably many other distinctions would be found upon disection of the flowers.

Brunfelsia dwyeri is very different from *B. undulata* Sw., which is widely cultivated in Panama. *Brunfelsia undulata* has a tube more than 6 cm long and a limb less than 5 cm across. Its flowers are white and fade to yellow. No other species of *Brunfelsia* are now known from Panama.

In the Cerro Azul-Cerro Jefe areas of central Panama this species appears as a remnant after mature forests have been cut. The region where most of the collections have been taken is 700–1000 m in elevation and has a seasonal rainfall pattern.

PANAMA. COCLE: Between Cerro Pilón and El Valle de Antón, alt. 700–900 m, cloud forest, *Duke & Dwyer 13933* (MO, GH). PANAMA: Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 471* (MO). Cerro Jefe, *D'Arcy 3948, 3959* (both MO); *Duke 9429* (MO). Forest edge and road bank, Cerro Jefe, alt. ca. 2,900 feet, *Dwyer & Gauger 7349* (MO), *7351* (GH, MO). Secondary cloud forest, summit of Cerro Jefe, *Dwyer et al. 5051* (MO). Along road from Cerro Azul to Cerro Jefe at 23–2700 feet, *Tyson 5313* (MO); *Tyson et al. 3312* (MO, type collection).

HISTOLOGY

To supplement the description of the gross morphology of *Brunfelsia dwyeri*, a brief study was made of its wood and leaf. Observations are based on a piece of branch, 2.1 cm across, from *Dwyer et al. 5051*. In general appearance, the wood has a fine, homogenous grain and is very difficult to work.

WOOD

Topography diffuse porous.

Vessels numerous, ca. 135 mm^2. Distribution mostly solitary with occasional groups of 2–4, more often in tangential than in radial orientation. Diameter very small, 25–48μ (tangential measurement), rather uniform. Pores elliptical, mostly more or less radially aligned, only slightly angular. Length of medium size; 400–700(–1000)μ; mean of 50 measurements, 586μ. Endwall measured from transverse 45° to 80°. Perforations simple and margined. Tails sometimes elongate. Intervascular pitting mostly alternate, or rarely opposite, sometimes in more or less vertical rows. Pits uncrowded, bordered with oblique aperatures, circular or very slightly elliptical, 5–7μ long. Tyloses or other contents not observed.

Rays very numerous, 12–16 per mm, distinctly dimorphic (Kribs heterogenous Type I but without very long uprights): uniseriates low of height to 15 cells, to 1.25 mm, width to 25μ; heterocellular multiseriates moderately fine, to 38μ wide and 2–3 cells wide of upright (120μ high), square (55μ) and procumbent (25–32μ wide and 5–50μ long) cells. Vessel-ray pitting uncrowded, alternate or opposite, more variable in size than intervascular pits, 4–8μ wide, mostly oblate, half-bordered. Ray cells contain an amorphous, colorless, noncrystalline substance.

Axial parenchyma extremely scanty with the same sort of contents as the rays.

Imperforate tracheary elements medium sized fibre tracheids; (62–)870–1200(–1400)μ long; mean of 50 measurements, 994μ. Pits plentiful, scattered, with occasionally long and conspicuous extended aperatures.

Structure unstoried.

LEAF

Stomata confined to the dorsal (abaxial) surface, 37–50μ long, of a cruciferous type (if the definitions of Airy Shaw *in* Metcalfe & Chalk, *Anatomy of the Dicotyledons*, 1: xv, are used, anisocytic, anomocytic, and paracytic types must be said to occur with about equal frequency on the same leaf).

Druses 140–190μ across scattered regularly in the leaf parenchyma, each contained within the limits of a single, usually enlarged cell.

The wood anatomy is unspecialized, moreso than might have been expected for a supposedly advanced member of the advanced Tubiflorae. Heterocellular rays, fibre tracheids, sloping vessel endwalls and unstoried wood are generally regarded as primitive wood features. Absence of axial parenchyma is an uncommon feature of dicotyledonous woods, and in *Brunfelsia dwyeri* it is almost absent. This case does not accord well with Carlquist's (Ann. Missouri Bot. Gard. 56: 383. 1969) finding that "consistent formation of parenchyma seems characteristic of longer-lived species in Goodeniaceae" where absence of axial parenchyma is confined to relatively short-lived perennials from Australia. One might speculate that axial parenchyma was primitively absent from *Brunfelsia* but has been reduced to absence in the Goodeniaceae; or that there may be more than one set of conditions leading to reduction of axial parenchyma.

Much of this work, including some of the collections for this species description, was supported by NSF grant GB-5674 (Principal investigator Walter H. Lewis). Assistance by R. Keating, Southern Illinois University, Edwardsville, in preparation and examination of the wood and leaf sections is gratefully acknowledged.—*W. G. D'Arcy, Missouri Botanical Garden.*

NEANOTIS PRAINIANA (W. A. TALBOT) W. H. LEWIS TO *OLDENLANDIA* (RUBIACEAE)

Critical study of the holotype of Talbot's *Anotis prainiana* (INDIA. MYSORE STATE: Santaveri 5500 ft. altitude, Kadur district, *Talbot 2995*, Talbot Herbarium collection, BSI) reveals that the species is not a member of Asiatic *Neanotis* W. H. Lewis (*Anotis* auct. non DC.). It belongs to *Oldenlandia*. This is confirmed by further study of recent collections from other hilly parts of Mysore State.

OLDENLANDIA PRAINIANA (W. A. Talbot) Craib, Kew Bull. 1910: 278. 1910.
Anotis prainiana W. A. Talbot, Jour. Bombay Nat. Hist. Soc. 11: 237. *t.* 6. 1897.
Neanotis prainiana (W. A. Talbot) W. H. Lewis, Ann. Missouri Bot. Gard. 53: 40. 1966.

—*K. Hemadri, Botanical Survey of India, Poona. 1. India.*

The 1970 Jesse M. Greenman Award

The recipient of the 1970 Greenman Award is Beryl Simpson Vuilleumier, Harvard University. The award winning publication is "The systematics and evolution of *Perezia* sect. *Perezia* (Compositae)" (Contr. Gray Herb. 199: 1–163).

The Greenman Award is presented annually by the Alumni Association of the Missouri Botanical Garden. It recognizes the best paper in plant systematics published during the previous year and based on a Ph.D. dissertation. Papers published in *1970* are now being considered. Reprints of such papers may be submitted to David M. Gates, Director, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110, for consideration.—*Editor.*

The F. B. and B. A. Krukoff Memorial Fund

Through the generosity of Dr. and Mrs. Krukoff, the Missouri Botanical Garden is able to purchase herbarium specimens originating from Africa, the Middle East (Turkey to Iran), and Australia. Anyone possessing determined duplicate specimens should consider the availability of these funds to help offset collecting expenses.

Individuals or institutions who have material from the aforementioned areas should write to Dr. Walter H. Lewis, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.—*Editor.*

Erratum: Ann. Missouri Bot. Gard. 56: 295, line 8. For "The December" read "The February."

The previous issue of the Annals of the Missouri Botanical Garden, Vol. 57, No. 1, pp. 1–134, was published on December 2, 1970.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum*.

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

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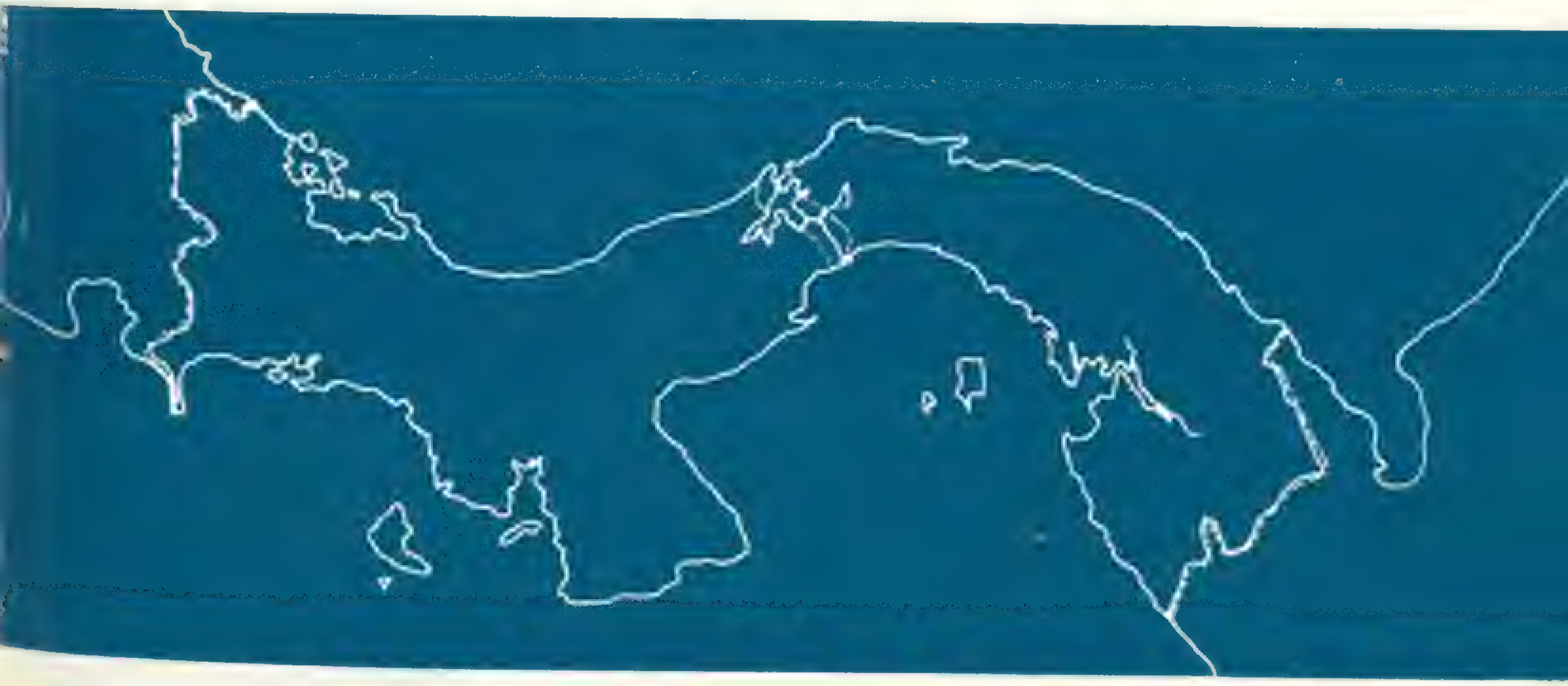

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OSMOTIC CHARACTERISTICS OF TISSUE FLUIDS IN THE SAHUARO GIANT CACTUS (*CEREUS GIGANTEUS*)[1]

OSCAR H. SOULE[2] AND CHARLES H. LOWE[3]

ABSTRACT

Osmotic pressure of sahuaro cortex tissue fluids changed significantly during the fall and winter of 1966 67 through the range of the sahuaro giant cactus (*Cereus giganteus*). At the northern end of the geographic distribution, the osmotic concentration decreased significantly from 320 mOsm in September to 185 mOsm in January. At the southern geographic limit, southern Sonora, the osmotic concentration increased significantly from 190 mOsm in September to 350 mOsm in February. In southern Arizona the osmotic concentration also increased significantly from 190 mOsm to 320 mOsm over the same period. In southern Arizona, osmotic pressure of cortex fluids decreased with increasing elevation. A significant difference in the osmotic pressure of the fluids on the south side (higher) and north side (lower) of sahuaros in all populations with increasing osmotic concentration was found. This difference did not exist when the sahuaros were in an advanced state of hydration. Indications of genetically fixed hardiness factors exist within the sahuaro populations; however, more thorough examination was beyond the sensitivity of monitoring the osmotic pressure. Changes in osmotic pressure of sahuaro cortex tissue fluids were related to effective precipitation and influenced by environmental temperatures. Within the ecological range of the sahuaro, conditions involving close interaction of low temperature and high precipitation become limiting to the distribution of this species.

Temperature and precipitation have long been considered important factors in the distribution of the sahuaro, *Cereus giganteus* Engelmann (Shreve, 1911, 1914, 1951; Turnage & Hinckley, 1938; Lowe, 1959, 1966, 1967*a*; Niering, Whittaker & Lowe, 1963; Hastings & Turner, 1965). One or both of these parameters in the extreme state appear to be specifically limiting to the sahuaro on at least three of the four edges of its range (Lowe, 1959). Since both have a pronounced effect on the osmotic concentration of plant tissue fluids, the

[1]Invaluable assistance in the field aspect of this project was volunteered by James L. Patton and Michael D. Robinson. We also thank Robert L. Bezy and Eldon D. Braun for their help in Sonora, Mexico. Thanks are due Dr. Richard S. Felger for assisting with plant identifications, and Dr. Roy E. Cameron for his cooperation in obtaining the detailed soil analysis at the Jet Propulsion Laboratory in Pasadena, California.

Special acknowledgment is given Dr. Peter J. Lardner for his help in the initial stages of this problem and Richard D. Krizman for his partnership in the examination of the geographical range of the sahuaro. The manuscript was read by Drs. Howard K. Gloyd, James W. O'Leary, Edwin B. Kurtz, and Wayne R. Ferris. Their critical comments are greatly appreciated.

Support has been provided through National Park Service Grant 14-10-0333-1303 on Saguaro Ecology.

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FIGURE 1.—Cerro Prieto, Sonora, Mexico, monitoring site.—A. Sahuaro #179 above exposed volcanic rubble. Little vegetation is found on the exposed areas and only minimal soil formation is taking place.—B. Sahuaro #178 in the dense thornscrub short-tree forest near the top ecotone of Cerro Prieto. Photos taken 13 October 1966.

osmotic pressure of the fluid of sahuaro cortex tissue was monitored for changes during the fall and the winter of 1966–67. A latitudinal transect was taken from extreme northern populations (northern Arizona) to the extreme southern populations (southern Sonora), and another transect was made along an elevational gradient (Santa Catalina Mountains, Tucson, Arizona) near the center of maximum sahuaro density (southern Arizona).

The sahuaro represents the farthest northward extension of any member of one of the most distinct groups in the cactus family, the subtribe Cereinae (Hutchinson, 1967). Its unique ability to penetrate as far into North America as it does suggests that examination of samples at the edges and throughout its range would show the ability of inherent mechanisms to cope successfully with extreme environmental conditions that are otherwise limiting, genetic abilities present in adjacent forms that do not occur naturally in this area.

METHODS

Selection of Sampling Sites. Northern and southern site locations in northern Arizona and in southern Sonora represent the natural latitudinal extremes for the sahuaro. The sites in the Tucson region on the bajadas of the Tucson Mountains and the Santa Catalina Mountains represent sahuaro populations of high density. Also on the Santa Catalina Mountains an elevational transect was established from 817 meters to 1317 meters, near the upper elevational limit of the sahuaro.

FIGURE 2.—Cerro Masiaca, Sonora, Mexico, monitoring site.—A. Sahuaro #0-165 on south-facing hillside which opens onto the valley of the Río Masiaca. Coastal foothills of the Sierra Madre Occidental are in the background.—B. The vegetation at the top of the Cerro Masiaca in the study area, dominated by thornscrub species. The giant cacti present are *Cereus giganteus* (sahuaro), *Cereus thurberi* (organpipe), *Cereus pecten aboriginum* (hecho). The highway in the background beyond the hill is Mexican Highway 15, and the Gulf of California is on the horizon. Photos taken 21 September 1966.

Selection of Sampling Dates. The series of consecutive sampling dates, September 1966–February 1967, was selected to monitor change in the osmotic pressure of sahuaro tissue fluids during the fall and winter seasons. Winter is the season during which the sahuaro is subjected to more sub-zero (° C) temperatures than any other columnar giant cactus, a situation which might appear to be more limiting to the other species, but is eventually limiting to the sahuaro as well.

Osmotic pressure was monitored since it reflects change in the freezing point depression of sahuaro fluids. The freezing-point depression (° T) of the plant tissue becomes greater with increased resistance to cold. Osmotic pressure of expressed tissue fluid does not give the absolute value of the freezing point depression of the intact tissue. However, it does parallel changes in the absolute value at a level of approximately one tenth the absolute value. Therefore, change in osmotic concentration was used in the determination of change in the water relations of the sahuaros under natural conditions.

Selection of Plants. The majority of plants sampled (81 of 86) were two meters or more in height. Individuals selected were not obviously diseased and had no extensive insect damage to the trunk. They were numbered with aluminum tags wired around the base of the tree, and the height and number of arms were recorded.

During the period of monitoring between September 1966 and February 1967, 86 sahuaros were sampled 234 times—23 were sampled 61 times in southern Sonora, 39 were sampled 108 times in southern Arizona, and 24 were sampled 65 times in northern Arizona. Three plants died during the period of monitoring, and one died subsequently.

The sampling pattern avoided interference due to healing responses to the incisions by the sahuaros. Some individuals were sampled at one to five month intervals, and others were sampled every month. Also one or more were sampled for the first time throughout the period to introduce values from otherwise completely unsampled individuals. These three types of sampling gave similar values. Plants being sampled for the sixth time in six months had concentrations within the range of variation of those being concomitantly sampled for the first time.

Sampling of Plants. Samples were taken from the south and north sides of each sahuaro. Direction was determined with a Leupold compass. All samples were taken at 1200 hours ± 1 hour with few exceptions. The height at which samples were taken was 2 ± 0.5 m or the middle of the plant, whichever was lower.

Vertical incisions were made at the bottom of each side of the pleat and in at an angle towards the woody ribs. Then cuts were made across the pleat about 5 cm apart. This separated a pie-shaped wedge from the sahuaro. The apex of the wedge came from near the ribs, and the opposite side was the cuticle and epidermal tissue.

The apex of the wedge was removed with a sharp knife, and a sterile glass slide was drawn across the freshly exposed surface. The fluid thus collected (*ca.* 0.2 ml) was poured directly into a custom 0.2 ml osmometer tube (Advanced Instruments, #3124), which was corked and frozen on dry ice. The time between exposure of the fresh surface and the freezing of the fluid was approximately 20 seconds. The time between the removal of the wedge from the plant and completion of the sampling was approximately two minutes. When possible two samples were taken from the wedge.

After the fluid was poured into the test tube, the tube was capped with a numbered cork and the tree number, direction of side and cork number were recorded. The tube was immediately placed in a rack on dry ice in a styrofoam cylinder. This cylinder, 30 cm × 22.5 cm with a wall thickness of 3.5 cm, maintained a temperature gradient from −80° C (inside) to +60° C (outside) for several hours with two pounds of dry ice, permitting frequent openings of the cylinder to insert samples.

The September samples represent arms of sahuaros which were transported to Tucson where similar fluid collection methods were used.

Osmometry. The frozen 0.2 ml samples were brought to the osmometer which was set up in buildings in Navojoa, Tucson, and Wikieup during each sampling run. An Advanced Instruments (AI) freezing point osmometer (Model 66 3II AS, #3023) was used for determination of osmotic concentration. The instrument has a repeatability of ±1 milliosmol (mOsm). It was calibrated with fresh NaCl standards of known concentration.

After calibration of the osmometer the samples were thawed at room temperature, and the osmotic pressure of the fluid directly determined with the osomometer. The thermometer probe (AI #3153S) and the stir wire (AI #3H243) were rinsed with distilled water and wiped dry with a soft sterile towel.

Soil. Soils discussed under Habitats were collected during the summer of 1965. A full

FIGURE 3.—Saguaro National Monument, Tucson Mountain Section, Pima County, Arizona, monitoring site. Sahuaro cactus forest (sahuaral) on western bajada of the Tucson Mountains. Shrubs in the foreground are *Franseria deltoidea* with scattered *Opuntia*. Trees in the background are *Cercidium microphyllum* and *Olneya tesota*. Sahuaro #0-144 in left center (3.0 m). Photo taken 29 July 1968.

series of tables are given supplementary publication through the American Documentation Institute, Auxiliary Publication Project, Photoduplication Service, Library of Congress, Washington, D.C. 20525. They may be ordered as photostats and as microfilm by check or money order made out to Chief, Photoduplication Service, Library of Congress. Analysis of these soils was carried out by the Jet Propulsion Laboratory in Pasadena, California. The mechanical soil analysis of the Santa Catalina elevational transect (Fig. 36, Table 13) was determined with standard soil testing sieves.

Climate. Sonoran weather information was taken from Secretaria de Recursos Hidraulicos (1952) and Hastings (1964), as well as official records supplied by the Secretaria de Recursos Hidraulicos, Dirección de Hidrologia, Departmento de Hidrometria, Oficina de Climatologica in Navojoa, Sonora.

Weather information for Tucson was taken from Department of Commerce (1966*a*; 1967*a*) and Department of Commerce (1966*b*; 1967*b*). Weather information for Wikieup, Arizona was taken from Department of Commerce (1966*a*; 1967*a*).

Laboratory calibrated Taylor maximum-minimum self-registering thermometers, #5438, were used to obtain the data presented in Table 12.

Statistical Methods. Standard statistical methods, including Chi-square test and Student's *t*-test, were used to determine the significance of difference between samples (Simpson, Roe & Lewontin, 1960). Probabilities for Chi-square tests were used in comparisons of the climatological data. Two *t*-tests, for frequency distribution and for paired comparison analysis, were used to determine the significance of difference in osmotic concentrations, the former being graphed by the Dice-Leraas method.

FIGURE 4.—Gate's Pass, Pima County, Arizona, monitoring site. Sahuaro #0-142. Golden Gate Mountain in the background (1307 m). The understory of the vegetation in the foreground is dominated by *Franseria deltoidea*, *Krameria parvifolia*, and *Tridens puchellus*. The upper stratum contains *Cercidium microphyllum* and *Fouquieria splendens* in addition to *Cereus giganteus*. Photo taken 29 July 1968.

HABITATS

SOUTHERN SONORA

Site Location. Two sites in southern Sonora, at the extreme southernmost distribution of the sahuaro, were monitored for changes in osmotic pressure from September 1966 through February 1967. The southernmost, Cerro Masiaca, is 23.8 miles south of Navojoa, Sonora, Mexico, by Mexican Highway 15; 109° 10′ W, 26° 45′ N, elevation 188 m (Fig. 2). The other site is Cerro Prieto, at 9.3 miles east of Navojoa on the Alamos Highway; 109° 18′ W, 27° 06′ N, elevation 295 m (Fig. 1).

Site and Area Desciption. Differences in the general ecology of the two sites are relatively minor. The vegetation is typical of the subtropical thornscrub (Lowe, 1967*a*), or thorn forest (Gentry, 1942), as represented on volcanic slopes. The coverage is high (up to 70–95%) and dominated by drought decidious trees and columnar cacti, where not entirely open due to unstable rocky substratum. These sites represent the conditions at the extreme southern end of the goegraphic range of the sahuaro (*Cereus giganteus*). Along with the sahuaro, the dominant species include *Cercidium praecox, Cereus pecten-aboriginum, Cereus thurberi, Fouquieria*

macdougalii, Lysiloma divaricata, Pithecellobium sonorae, and *Prosopis torreyana.* The understory is composed of short grasses, *Acacia cymbispina, Bursera odorata, Bursera laxiflora, Caesalpinia palmeri, Lycium, Opuntia fulgida, Peniocereus johnsonii, Randia,* and *Rathbunia alamosensis.*

At the specific level, most of the mammal fauna at these sites is common to the Sonoran Desert. However, such species as *Neotoma phenax* (Sonoran Wood Rat) and *Balantiopteryx plicata* (Peters' Bat) represent a subtropical influence that does not reach the desert proper. Goldman's (1951) Mayo Biotic District of the Sonoran Biotic Province describes this well. The characteristic amphibians and reptiles of this area are listed by Bogert and Oliver (1945). Again there are subtropical species which are not found much farther north such as *Heloderma horridium* (Mexican Beaded Lizard) and *Bufo mazatlanensis* (Mazatlan Toad), but the majority of the species are shared with the Sonoran Desert. Especially conspicuous is the large number of species of birds found here. These have been described by Rossem (1931) as characteristic of the thornscrub in his delimitation of the broad Alamos Faunal District.

The overall geographic distribution of the wide diversity of vertebrate species that occur at these sites in the thornscrub indicates the broad ecotonal nature of this habitat. This is to be expected of such a habitat located in the continuum from the subtropical short-tree forest to the south to the desert to the north.

Soil. The hills of these sites are a result of the wide spread Upper Tertiary volcanic activity in the area (Gentry, 1942). The surface of the upper slopes is composed of basaltic rocks and boulders, while the substratum at the base is a sandy loam.

TABLE 1. Mechanical analysis and textural class of soils sampled along the latitudinal transect through the geographic range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto, Sonora, Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountain Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Mechanical Analysis (per cent composition) Sand (2.0–0.02mm)	Silt (0.02–0.002mm)	Clay (0.002mm or less)	Textural Class
Southern Sonora	Surface–3cm	74	24	2	loamy sand
	3cm–15cm	52	40	8	sandy loam-loam
Southern Arizona	Surface–5cm	84	13	3	loamy sand
	5cm–15cm	78	17	5	loamy sand
Northern Arizona	Surface–3cm	70	27	3	sandy loam
	3cm–15cm	74	23	3	loamy sand

A detailed soil analysis was made from soils sampled at the base of Cerro Prieto, both from the soil surface and from a depth of 15 cm. The surface soil is a loamy sand, and with the increase in smaller particle size the structural class changes to a sandy-loam loam at 15 cm (Table 1). The percentages of silt (40%)

and clay (8%) are the highest of those at any of the sites examined in Arizona or Sonora during the present study.

Increase in the water-holding capacity of the soil, both at levels available and unavailable to the plants, is increased by these smaller particle sizes. The maximum water holding capacity of this soil is greater than that at the other sites examined (Table 2). This is also true of the water holding capacity against increasing pressures (Table 2).

TABLE 2. Moisture constants for soils along the latitudinal transect through the geographic range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto, Sonora, Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountains Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Moisture Constants (per cent water) Maximum Water Holding Capacity	0.1 Bar	0.5 Bar	15 Bar
Southern Sonora	Surface–3cm	49	45.6	27.7	19.9
	3cm–15cm	45	40.6	33.1	19.9
Southern Arizona	Surface–5cm	27	18.6	10.7	4.6
	5cm–15cm	35	23.2	14.6	5.4
Northern Arizona	Surface–3cm	21	15.9	10.8	7.2
	5cm–15cm	24	16.6	12.3	7.6

The darker substratum at the base of Cerro Prieto is characteristic of the southern geographic distribution of the sahuaro. The wet and dry reflectivity values are the lowest of any obtained along this geographic transect (Table 3). The volcanic origin and basaltic nature of the substratum contributes to the darker coloration. This is important in recognizing the total heat load to which the sahuaros are subjected, and it is especially so for the smaller plants.

The pH of the soil (8.0, soil paste; 7.8, soil-water extract, see Table 4) is in the range of that considered neutral for soil (Leeper, 1948). It is the neutral to alkaline condition that is to be expected for arid regions (Millar, Turk & Foth, 1958).

The buffer capacity of this soil is also quite high (13.5 meq/100 gm, see Table 5) in comparison with the other soils examined. Soil is generally buffered by organic and inorganic colloidal material, although salts such as carbonates and phosphates may be used. The high organic content of the soil from the base of Cerro Prieto, as well as the total carbon, total nitrogen, organic carbon, organic nitrogen, and carbonate carbon (Table 6) suggest sources for the greater buffer capacity. The higher organic content of the soil at this site reflects the greater biomass of vegetative cover in this region, and a greater effective decomposition and retention of the associated litter than occurs in thornscrub habitats.

TABLE 3. Soil color, Munsell notation, and reflectivity of wet and dry soil samples collected along the latitudinal transect through the geographic range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto Sonora, Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountains Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Color and Munsell Notation[a] Wet	Dry	Reflectivity[b] Wet	Dry
Southern Sonora	Surface–3cm	dark gray 5YR 4/1	gray 5YR 5/1	6	18.5
	3cm–15cm	dark reddish gray 5YR 4/2	gray 5YR 5/1	6	14
Southern Arizona	Surface–5cm	dark reddish gray 5YR 4/2	light yellowish brown 10YR 6/4	8	22.5
	5cm–15cm	dark brown 7.5YR 4/4	yellowish brown 10YR 5/4	7	17
Northern Arizona	Surface–3cm	reddish brown 5YR 4/4	light yellowish brown 10YR 6/4	9	33.5
	3cm–15cm	brown 7.5YR 4/4	pale brown 10YR 6/3	12.5	32

[a] Sieved sample [b] Method of zero suppression

SOUTHERN ARIZONA

Site Location. Eight sites, all in the vicinity of Tucson, Pima County, Arizona, were monitored for change in osmotic pressure of sahuaro tissue fluids in southern Arizona. Two of these were in the Tucson Mountains, and six were in the Santa Catalina Mountains.

The two sites in the Tucson Mountains (1428 m) were located on the western bajada of this range and were on western or southwestern exposures. One site (Tucson Mountains, Saguaro National Monument) was in Saguaro National

TABLE 4. Hydrogen ion concentration (pH) for saturated soil paste and soil-water extract of soil samples collected along the latitudinal transect through the geographic range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto, Sonora, Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountain Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Saturated Soil Paste	Soil-Water Extract (1:5)
Southern Sonora	Surface–3cm	8.0	7.8
	3cm–15cm	8.0	7.8
Southern Arizona	Surface -5cm	7.0	6.9
	5cm–15cm	6.8	6.8
Northern Arizona	Surface–3cm	8.2	7.8
	3cm–15cm	8.0	7.8

Monument, Tucson Mountain Section (T13S, R11E, Sect. 27, NW¼, elevation 724 m). The other (Tucson Mountains, Gate's Pass) was located at the northwestern base of Golden Gate Mountain (1307 m), south of West Speedway near the western base of Gate's Pass (T14S, R12E, Sect. 15, NW¼, elevation 851 m).

Five of the six sites in the Santa Catalina Mountains (2792 m) were on the elevational transect which followed the Mount Lemmon Highway from 817 m (alluvial flats) to the uppermost accessible group of sahuaros (1317 m) on this transect. The coordinates and elevation for the sites on the transect are listed in Table 7. The sixth site (Santa Catalina Mountains, foothills) was at the southern base of the Santa Catalina Mountains between Pima Canyon and Finger Rock Canyon at the north end of Campbell Avenue, Pima County, Arizona (T12S, R14E, Sect. 33, SE¼, elevation 907 m).

TABLE 5. Buffer capacity for soils collected along the latitudinal transect through the geographic range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto, Sonora, Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountains Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Buffer Capacity meq/100gm
Southern Sonora	Surface–3cm	13.5
	3cm–15cm	13.5
Southern Arizona	Surface–5cm	0.5
	5cm–15cm	0.5
Northern Arizona	Surface–3cm	8.0
	3cm–15cm	6.5

Site and Area Description. The site monitored in the Saguaro National Monument, Tucson Mountain Section, is in the Arizona Upland of the Sonoran Desert (Shreve, 1951). It lies on the western bajada of the Tucson Mountains facing the south-north drainage of the Avra Valley which feeds into the Santa Cruz River through Brawley Wash (Fig. 3). It is situated in the upper part of the edaphically controlled ecotone between the *Larrea* vegetation type of the Avra Valley and the *Cercidium* vegetation type of the Tucson Mountains (Yang, 1957; Yang & Lowe, 1956).

The characteristic tree-like species include *Cereus giganteus, Cercidium microphyllum, Prosopis juliflora,* and *Olneya tesota.* Large shrubs such as *Acacia constricta, A. greggii, Celtis pallida, Fouquieria splendens, Larrea divaricata,* and *Simmondsia chinensis* dominate the well-developed understory. Shorter members of the understory include *Calliandra eriophylla, Encelia farinosa, Franseria deltoidea,* and *Jatropha cardiophylla.* Numerous members of the Cactaceae also found in the understory are species of *Echinocactus, Echinocereus, Mammillaria,* and *Opuntia.*

FIGURE 5.—Santa Catalina foothills monitoring site, Pima County, Arizona. Desertscrub, Lower Sonoran. Typical middle bajada vegetation. The trees are *Cercidium microphyllum*. Two sahuaros in the foreground, #0-179 (on left) and #0-147 (on right), were sampled during the monitoring period. The Santa Catalina Mountains are in the background. Photo taken 7 July 1968.

The site location below the western base of Gate's Pass, Tucson Mountains, places it also in the Lower Sonoran Zone of the Arizona Upland on the western

TABLE 6. Content of organic matter and carbon and nitrogen values for soils along the latitudinal transect through the range of the sahuaro. Southern Sonora sample from the base of Cerro Prieto, Sonora Mexico; collected 11 July 1965. Southern Arizona sample from Saguaro National Monument, Tucson Mountains Section, Pima County, Arizona; collected 2 August 1965. Northern Arizona sample from 17.3 miles north of Wikieup, Mohave County, Arizona; collected 19 July 1965.

Site	Depth of Sample	Organic matter, auto-clave extract	Organic matter, organic carbon ×1.724	Total carbon	Carbon and nitrogen values Total nitrogen	Organic carbon	Organic nitrogen	Carbonate carbon
Southern Sonora	Surface–3cm	0.654	1.446	1.29	0.080	0.839	0.074	0.436
	3cm–15cm	0.589	1.083	1.40	0.046	0.628	0.052	0.725
Southern Arizona	Surface–5cm	0.350	0.293	0.194	0.016	0.170	0.014	0.010
	5cm–15cm	0.273	0.293	0.188	0.016	0.170	0.018	0.006
Northern Arizona	Surface–3cm	0.385	0.360	0.611	0.017	0.209	0.017	0.388
	3cm–15cm	0.169	0.467	1.260	0.017	0.271	0.013	0.985

FIGURE 6.—817 meter site on the Santa Catalina elevational transect, Pima County, Arizona. Typically open *Larrea* vegetation type with scattered sahuaros (#0-180 in the background). Mesquite are found along the small runoff channels with extremely tall creosotebush (*ca.* 3 m). Santa Catalina Mountains are on the horizon. Photo taken 7 July 1968.

bajada of the Tucson Mountains. The same plant species are dominant here as at the site in the Saguaro National Monument (Fig. 4).

The Santa Catalina foothills site is similar although not identical to those sites monitored in the Tucson Mountains with respect to the edaphic conditions and vegetation. This site is located on the south-facing slopes of the Santa Catalina bajada in contrast to the western exposure of Tucson Mountain sites (Fig. 5). It has been referred to specifically as typical upper bajada vegetation (see Whittaker & Niering, 1965: Tab. 2: IX, i). The large dominant species include *Cereus giganteus, Cercidium microphyllum,* and *Prosopis juliflora.* The understory contains *Acacia constricta, Calliandra eriophylla, Encelia farinosa, Fouquieria splendens, Haplopappus tenuisectus, Jatropha cardiophylla, Krameria parvifolia,* and *Opuntia.*

The vegetation and flora of the sites comprising the Santa Catalina elevational transect have been described in detail and discussed by Whittaker and Niering (1964, 1965) and Lowe (1967*b*). The 817 meter site represents middle bajada vegetation (Whittaker & Niering, 1965: Tab. 2: IX, j, k) with *Larrea divaricata* being the dominant species. Here *Larrea* shares dominance with

FIGURE 7.—869 meter site on the Santa Catalina elevational transect, Pima County, Arizona. —A. Sahuaros (#0-181 is in foreground), paloverde, and mesquite form the upper stratum in the upper bajada vegetation at the base of the Santa Catalina Mountains.—B. Soldier's Canyon in the background with paloverde-sahuaro community in foreground, including sahuaro #0-149. (Compare with Fig. 6 in Lowe, 1967*a*.) Photos taken 7 July 1968.

Prosopis juliflora in the small washes where there is runoff (Fig. 6). The height of the *Larrea* may reach over three meters. The most common plants in the sparse understory are *Zinnia pumila, Psilostrophe cooperi,* and *Tridens puchellus. Cereus giganteus* is present both in the pure *Larrea* stands and in *Larrea-Prosopis* associations in the washes. The site is *ca.* 2 miles south of the base of the Santa Catalina Mountains.

The 869 meter site lies slightly downslope and to the west of the opening of Soldier's Canyon and is southwest of the junction of the Mount Lemmon Highway and Soldier's Trail Road (Fig. 7). The vegetation here has been considered atypical of upper bajada vegetation because of the proximity of the canyon and its effects (Whittaker & Niering, 1965: Tab 2: IX, g, h). The numerous common species are listed by Lowe (1967*b*), and *Cereus giganteus* and *Cercidium microphyllum* dominate the upper layer, along with *Prosopis juliflora.*

The 1067 meter site is on a south-facing slope which is littered with decomposing granite rocks and boulders. There are several large rock faces (1 m × 2 m) and small overhangs which provide microhabitats (Fig. 8). Also, in more protected areas, mats of *Selaginella* up to 2–4 cm thick provide cover for plants and animals. The most common species of the upper stratum are *Cereus giganteus,*

FIGURE 8.—1067 meter site on the Santa Catalina elevational transect, Pima County, Arizona. Lower Sonoran desertscrub vegetation dominated by sahuaros (*Cereus giganteus*) and paloverdes (*Cercidium microphyllum*). Scattered large rock faces and decomposing granite boulders (background) provide protection for small sahuaros on this south-facing slope above the lower part of Molino Canyon. Photo taken 7 July 1968.

Cercidium microphyllum, and *Prosopis juliflora.* The open understory includes *Acacia greggii, Calliandra eriophylla, Condalia lycioides, Encelia farinosa, Fouquieria splendens,* and *Jatropha cardiophylla.* This area has been described by Whittaker & Niering (1965: Tab. 2: VIII, d, e, f) and Lowe (1967*b*).

At the 1170 meter site there was wide-spread tissue damage (scarring) from the freeze in January 1962. Sahuaros sampled here were in both protected and exposed portions on south-facing slopes above Molino Canyon. The exposed location was near the end of a south-facing extension which received no protection from either side (Fig. 9). Here all the sahuaros showed some scarring approximately 65 cm below the crowns on the south and southeast sides of the plants. The protected area was adjacent to the exposed area, and the elevation was approximately the same. Here the sahuaros showed no scarring. This was due to the canyon effect provided by the extension to the east and the normal curve of the mountains outward (south) to the west (Fig. 9). This site is still in the Lower Sonoran Zone of Arizona Upland as described by Lowe (1967*a*, 1967*b*).

TABLE 7. Coordinates and elevations of sahuaro cortex tissue fluid monitoring sites on the Santa Catalina elevational transect.

Site and Elevation	Township	Range	Section	Quadrate
817 meters	T13S	R15E	Sect 24	SW¼
869 meters	T13S	R16E	Sect 18	NW¼
1067 meters	T13S	R16E	—	—
1170 meters	T13S	R16E	—	—
1317 meters	T13S	R16E	—	—

The upper stratum of the vegetation is not as well developed in the exposed area as in the protected area. The dominant species include *Cereus giganteus, Prosopis juliflora,* and *Cercidium microphyllum,* the last being much reduced in size on the exposed slope. The understory includes *Acacia greggii, Agave schottii, Calliandra eriophylla, Echinocactus wislizenii, Encelia farinosa, Fouquieria splendens, Haplopoppus laricifolius, Jatropha cardiophylla, Opuntia engelmannii,* and *Opuntia versicolor.* This area has been described as the lower edge of the transition from desert-grassland to Sonoran Desert (Whittaker & Niering, 1965).

The uppermost site (1317 m) is in the transition from desert grassland to open oak woodland (Whittaker & Niering, 1965: Tab. 2: VII, b, c, d). It lies on the steep south-facing slope of Molino Canyon, *ca.* 0.7 mile below Molino Basin, Mount Lemmon Highway, Pima County, Arizona. This was the site of a severe range fire in the summer of 1967 which killed or severely damaged all the sahuaros which had been sampled (Fig. 10). Along with the sahuaro, other species present are *Quercus emoryi, Vaquelinia california, Agave schottii, Fouquieria splendens, Calliandra eriophylla, Jatropha cardiophylla, Erythrina flabelliformis, Prosopis juliflora,* and *Opuntia engelmannii.* The understory is dominated by *Agave schottii,* a localized edaphic situation controlled by the granitic soil (Whittaker & Niering, 1965). This transect represents the limits in distribution of the sahuaros from Sonoran Desert through grassland to open oak woodland.

FIGURE 9.—1170 meter site on the Santa Catalina elevational transect, Pima County, Arizona.—A. Exposed habitat; desertscrub, Sonoran Desert. The scarring *ca.* 60 70 cm below the crowns of the sahuaros is a result of the freeze of January 1962. Upper stratum of the vegetation poorly developed; the understory contains *Agave schottii*.—B. Protected habitat; south-facing slope grades down to Molino Canyon. No scarring from 1962 freeze. Density of sahuaros is greater, and upper stratum of vegetation is more fully developed with *Cercidium microphyllum*, *Prosopis juliflora*, and *Cereus giganteus* (#0-152, center left; #0-153, center right). Photos taken 7 July 1968.

The vertebrates found on the bajadas of the Tucson Mountains and Santa Catalina Mountains are generally characteristic of the Arizona Upland of the Sonoran Desert. The lack of isolating factors has caused little endemism in the area characterized by sahuaros in this region. However, the proximity of this location to the edge of the desert results in several species from the lower desert habitats terminating their eastern distribution on and/or near these bajadas. These species are unable to continue on up into the desert grassland. Examples include *Dipodomys deserti* (Desert Kangaroo Rat), *Dipsosaurus dorsalis* (Desert Iguana), *Crotalus cerastes* (Sidewinder), and *Urosaurus graciosus* (Long-tailed Brush Lizard).

The mammals present on the bajadas of the Tucson Mountains and Santa Catalina Mountains (Cockrum, 1960; Niering, Whittaker & Lowe, 1963; Lund, 1966) vary with edaphic conditions and vegetation patterns, but there are no species endemic to the area.

The herpetofauna is characteristic of the alluvial bajadas supporting paloverde-sahuaro and creosote bush associations near Tucson (Ruthven, 1907; Gloyd, 1937; Yang, 1957; Lowe, 1967*a*).

The birds of sahuaro communities near Tucson have been discussed from many points of view (Swarth, 1914; Brandt, 1951; Hensley, 1954; Selander & Giller, 1963; Krizman, 1964; Soule, 1964; Phillips, Marshall & Monson, 1964; Short, 1965; Lund & Steenbergh, 1966). The wide diversity of habitats, rather luxuriant vegetation, and routes of seasonal migration give Tucson and the Santa Cruz Valley a broad avifauna.

TABLE 8. Osmotic concentrations of sahuaro tissue fluids reported in the literature. Sources for data and methods indicated in body of table.

Author and reference	Method and value obtained	Conversion to atmospheres	Temperature of tissue	Date of sampling
Livingstone (1906)	$\Delta T = 0.42°$ C	5.54	25° C	Not given
Livingstone (1906)	Plasmolysis method	3.9–7.0	25° C	Not given
MacDougal & Cannon (1910)	Not given	6.78	25° C	Feb. 1910
MacDougal (1911)	Not given	7–10	—	Not given
Gortner & Hoffman (1922)	Refractive index = 1.34; $\Delta T = 0.505$	6.07	20° C	Not given
MacDougal (1925)	Not given	4.0–7.0	—	Not given
Harris (1934)	$\Delta T = 0.63$–0.72	7.6–8.6	—	4 July 1916
Walter (1964)	Not given	4.7–7.2	—	Not given
Soule (1969)	Freezing point osmometer (sahuaro = 161.7–358.4 mOsm)[a]	3.62–8.03	15–34° C	Sept. 1966–Feb. 1967

[a] Higher values for sahuaro cortex tissue were obtained outside the six months period of observation in the present study (424.7 mOsm; 435.8 mOsm, 8 August 1966, Tucson region).

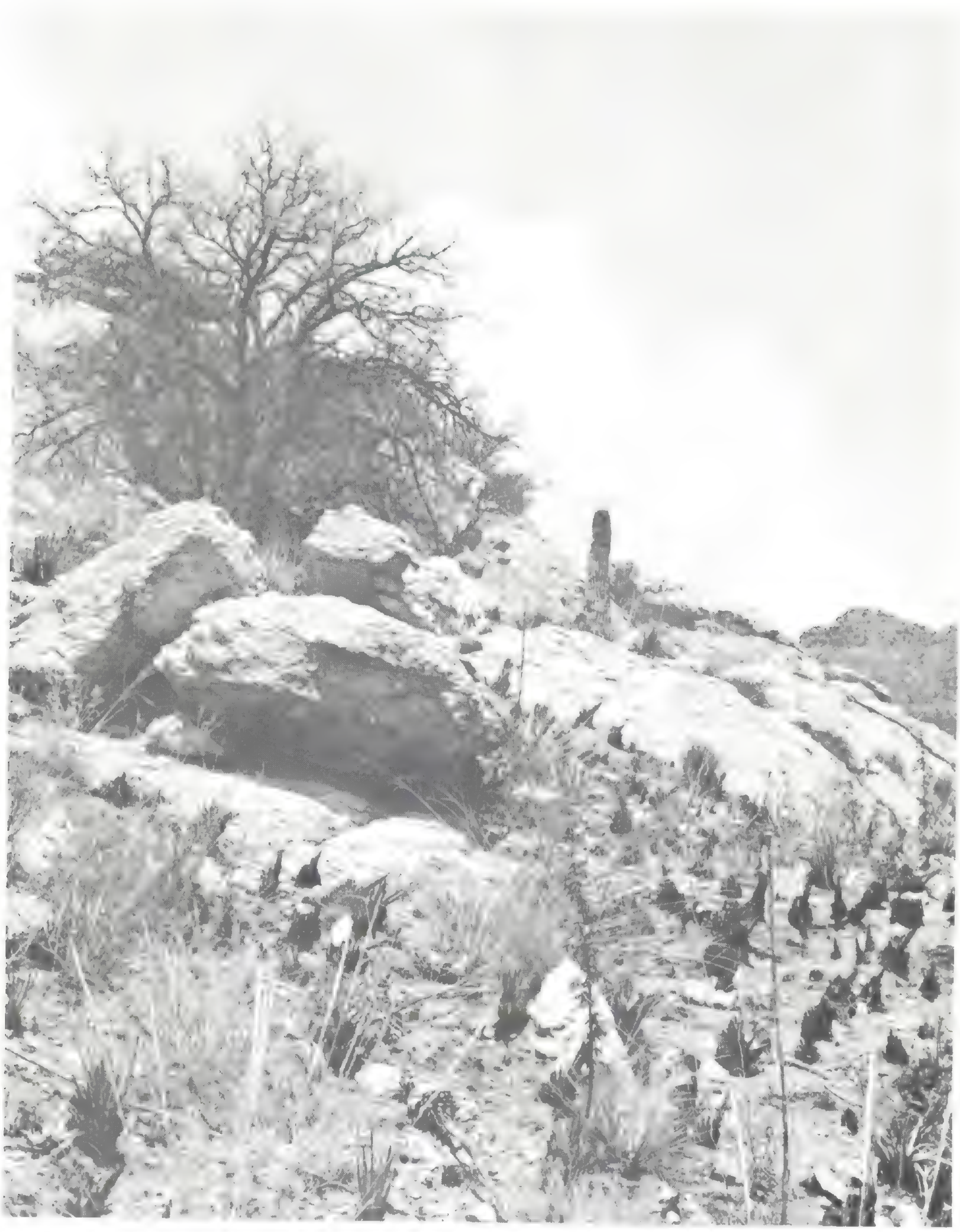

FIGURE 10.—1317 meter site on the Santa Catalina elevational transect, Pima County, Arizona. Transition from desert grassland to open oak woodland, Upper Sonoran. *Cereus giganteus* (#0-162), *Quercus emoryi,* and *Agave schottii,* (foreground) show effects of the summer range fire of 1967. Photo taken 7 July 1968.

Soil. The geology and soil of the sites monitored for changes in osmotic concentration of sahuaro tissue fluids have received extensive specific review by Yang (1957), Yang and Lowe (1956) and Whittaker and Niering (1965), as well as general review by Lowe (1967*a*).

The soil sample collected for southern Arizona came from Saguaro National Monument, Tucson Mountains Section. The site was about one half mile northeast of the intersection of Sandario Road and Golden Gate Road, Pima County, Arizona, elevation 716 m (T13S, R11E, Sect. 27, NW¼). The mechanical analysis of the soil placed it in the loamy sand textural class. The soil contained higher percentages of sand (2.0 to 0.02 mm) than any of the other soils examined (Table 1). The higher amount of sand particles was made up by a reduction in the amount of silt.

The moisture constants were intermediate for this soil even though the mechanical analysis showed that the soil of Saguaro National Monument, Tucson Mountains Section had 4–32% more sand and approximately one half to one third the silt of the soils from northern Arizona and southern Arizona (Table 2). At the highest pressure (15 bars = 14.8 atm) the soil from southern Arizona held the least moisture of the three soils, as would be expected due to the large particle size.

The color and reflectivity of both the wet and dry soil of southern Arizona was intermediate between values for northern Arizona (lightest color; greatest reflectivity) and southern Sonora (darkest color; lowest reflectivity) (Table 3). The reflectivity of the soil of the Saguaro National Monument, Tucson Mountains Section, was only one third to one half that of the soil from northern Arizona. This becomes significant immediately considering the similar coverage (15–60%) at the sites in northern Arizona and on the bajadas near Tucson.

The pH of the soil from Saguaro National Monument, Tucson Mountain Section, was slightly acid to neutral (Table 4). This is lower than would be expected from the reported values for soils from nearby sites (Yang, 1951). It is also lower than expected considering the low organic content and the amount of precipitation (Martin & Fletcher, 1943).

The buffer capacity of this soil was significantly reduced (Table 5). Reduced buffer capacity is to be expected of soils with high percentages of large particle size and/or low organic content. Coarse-textured soils are usually only slightly buffered (Millar, Turk & Foth, 1958). Also since the buffering materials of soils is present primarily in colloidal form, it is expected that soils high in organic content will be highly buffered, *e.g.*, the soil from southern Sonora (Table 5). The organic matter in the soil from Saguaro National Monument, Tucson Mountain Section, as well as amounts of total carbon, organic carbon and carbonate carbon, were well below similar values for the other soils examined (Table 6).

Northern Arizona

Site Location. Five sites were monitored for change in osmotic pressure around Wikieup, Arizona, between Wickenberg and Kingman, Arizona, on United States Highway 93. The northenmost site is 6.5 miles north of the Wikieup Post Office by Highway 93, Mohave County, Arizona; T16½N, R13W, Sect. 7, NW¼,

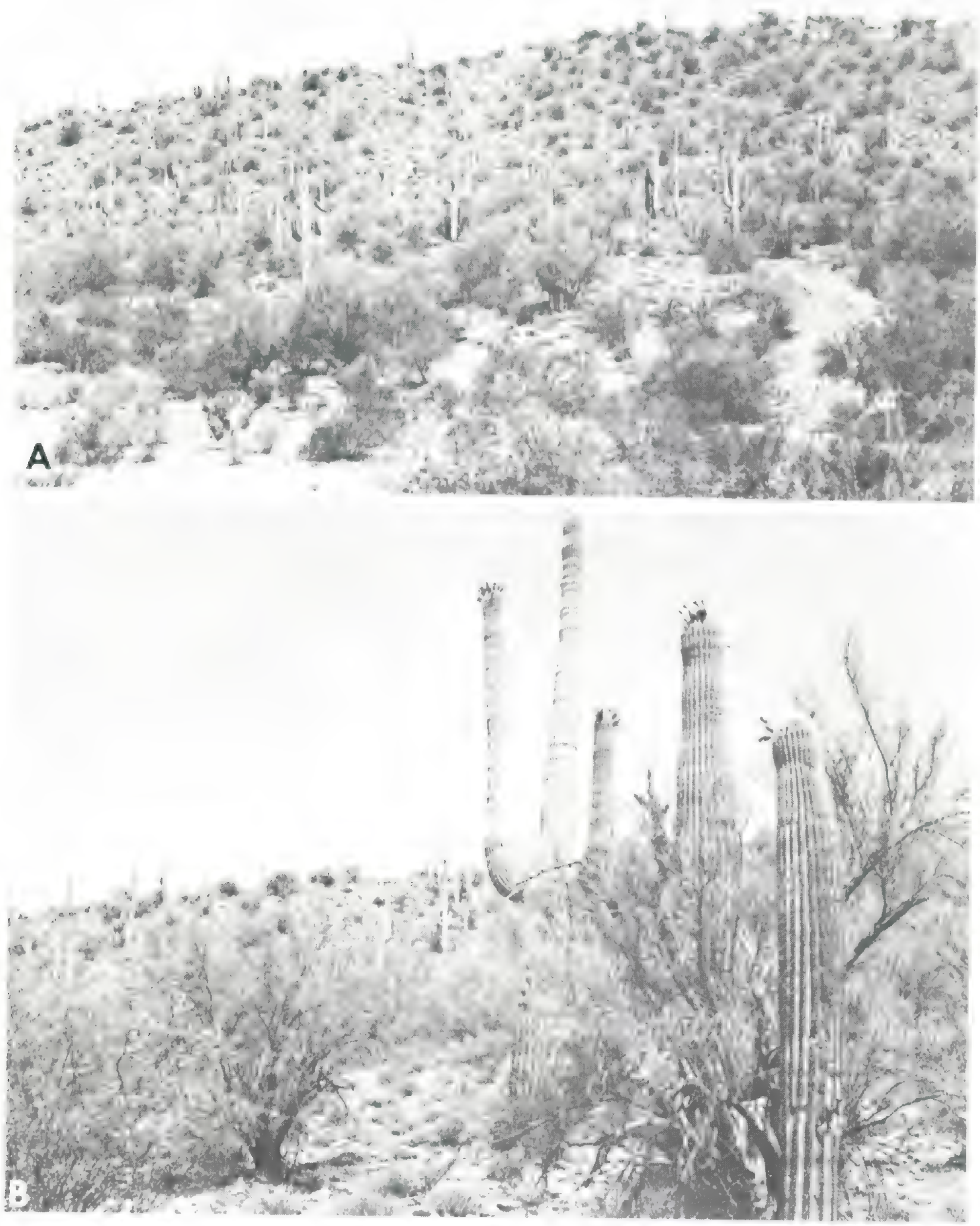

FIGURE 11.—Santa Maria River site, Yavapai County, Arizona. Desertscrub, Sonoran Desert. Lower Sonoran.—A. South-facing hillside bordering the Santa Maria River drainage. —B. Upper stratum dominated by *Cereus giganteus* (#186, left foreground) and *Cercidium microphyllum*; understory dominated by *Eriogonum fasiculatum*. Photos taken 4 July 1968.

TABLE 9. Osmotic concentration and date of maximum hydration, *i.e.*, minimum osmotic pressure, at all sampling sites during the period of monitoring, September 1966 February 1967.

Site	Minimum Concentration	Month and year
Cerro Prieto	161.7 mOsm	September 1966
Cerro Masiaca	195.7 mOsm	September 1966
Tucson Mountains (SNM)	194.3 mOsm	October 1966
Tucson Mts. (Gate's Pass)	186.5 mOsm	October 1966[a]
Catalina Foothills	188.1 mOsm	September 1966
Santa Maria River	183.4 mOsm	January 1967
Juniper Site	186.3 mOsm	January 1967
Burro Creek	190.0 mOsm	January 1967
South of Wikieup	191.4 mOsm	January 1967
North of Wikieup	177.0 mOsm	October 1966
	186.9 mOsm	January 1967
Catalina Mts. (817 m)	187.3 mOsm	September 1966
Catalina Mts. (869 m)	218.8 mOsm	September 1966
Catalina Mts. (1067 m)	206.9 mOsm	October 1966
Catalina Mts. (1170 m)	196.4 mOsm	September 1966
Catalina Mts. (1317 m)	191.0 mOsm	December 1966

[a] First sample

elevation 725 m. It lies in the drainage of the Big Sandy River between the Hualpai Mountains (2519 m) to the west and the Aquarius Cliffs (1585 m) to the east.

The south of Wikieup site is 5.9 miles south of the Wikieup Post Office by Highway 93, Mohave County, Arizona; T15N, R12W, Sect. 18, NE¼, elevation 616 m. It lies in the general area of Gray Wash, which drains into the Big Sandy River to the west.

The Burro Creek site is 0.2 mile south of the Burro Creek Bridge (Highway 93) over Burro Creek, and 8.1 miles north by road of the Mohave-Yavapai County line, Mohave County, Arizona; T14N, Sect. 20, NW¼, elevation 823 m.

The Juniper site is 1.0 mile north of the Mohave-Yavapai County line on Highway 93, Mohave County, Arizona; T13N, R10W, Sect. 7, NW¼, elevation 991 m.

The Santa Maria River site is 0.6 mile north of the Santa Maria River on Highway 93 and 10.9 miles south of the Mohave-Yavapai County line, Yavapai County Arizona; T12N, R19W, Sect. 21, NE¼, elevation 587 m. It lies on the north side of the Santa Maria River near the base of the south slope of Arrastra Mountain (1402 m) and opposite Ives Peak (1219 m) to the south.

Site and Area Description. The sites examined in northern Arizona followed the route of Highway 93. The first site, the lowest (Santa Maria River, 587 m), is in the valley of the Santa Maria River. The highway continues north over the granitic hills which mark the highest observed elevation for the northern distribution of sahuaros (Juniper site, 991 m). From this high point the elevation along the route of the highway decreases (Burro Creek, 823 m) until the drainage of the Big Sandy is approached (south of Wikieup, 616 m). The elevation once again increases in following the course of the Big Sandy upstream (north of Wikieup, 725 m) until the last sahuaro is reached (933 m). The vegetation

FIGURE 12.—Juniper site, Mohave County, Arizona. Juniper-oak Woodland. Upper Sonoran.—A. Large granitic boulders litter the habitat. Species present include *Cereus giganteus* (#0-197, left; #0 171, right), *Juniperus monosperma, Fouquieria splendens* (on horizon), *Yucca,* and *Nolina bigelovii* (inflorescence on the right horizon).—B. Close-up of sahuaro #0-171 with *Juniperus monosperma* and *Nolina bigelovii,* both are dominant species with the sahuaro. The elevation, 991 m, is the highest of the sites monitored in northern Arizona. Photos taken 18 June 1968.

TABLE 10. Osmotic concentration of tissue fluids on the south side and north side of sahuaro #184; Cerro Masiaca, Sonora, Mexico. September 1966–December 1966.

Month	Difference
September	3 mOsm
October	10 mOsm
November	29 mOsm
December	54 mOsm

beyond this point grades into typical chaparral in the upper valley in the foothills of the Hualpai Mountains (Humphrey, 1964).

As in southern Sonora the extreme geographic limits of the sahuaro in northern Arizona are in an ecotonal area. Here the range of two of the most characteristic plants of two major deserts help define the zone of over-lap between the Sonoran and Mohave Deserts (*Cereus giganteus* = Sonoran Desert and *Yucca brevifolia* = Mohave Desert). In this region the more arborescent aspect of the plant community is dominated by Sonoran Desert representatives, and the shrubs present are more characteristic of the Mohave Desert (Lowe, 1967*a*).

With change in topography there is a natural change in the general ecology of the sites. South of the Santa Maria River sahuaros are found with large numbers of Joshua trees. Where this occurs the sahuaros are advancing off the south-facing slopes of rocky hillsides onto the more level alluvial terrain which supports one of the largest Joshua tree forests in Arizona. On the slopes bordering the Santa Maria River the sahuaros become the more dominant of the two species and retain this dominance throughout the remainder of the transect. At the Santa Maria River site (587 m) the vegetation has an open structure with scattered trees and shrubs on the rocky south-facing slopes (Fig. 11). The characteristic plants are *Cereus giganteus, Acacia greggii, Calliandra eriophylla, Cercidium microphyllum, Encelia farinosa, Ephedra, Eriogonum fasciculatum, Franseria dumosa, Krameria parvifolia, Larrea divaricata, Lycium, Opuntia acanthocarpa, O. basilaris, O. phaecantha,* and *Prosopis juliflora.*

The highest site which was monitored for change in osmotic pressure in the northern distribution of the sahuaro was 991 m (Juniper site). Here the sahuaros are scattered over the rocky substratum spotted with granitic boulders (Fig. 12). The plant community includes several well known Upper Sonoran species (*Juniperus monosperma, Nolina bigelovii, Quercus turbinella,* and *Rhus trilobata*) as well as *Cereus giganteus, Acacia greggii, Condalia lycioides, Canotia holocantha, Echinocereus engelmannii, Eriogonum fasciculatum, Fouquieria splendens, Hymenoclea monogyra, Gutierrezia sarothrae, Krameria parvifolia, Larrea divaricata, Opuntia acanthocarpa, O. basilaris, O. phaecantha, Psilostrophre cooperi,* several grasses, and *Eriogonum inflatum.*

With the decrease in elevation, the vegetation at the Burro Creek site (823 m) lacks the Upper Sonoran elements which were found at the Juniper site. The substratum is littered with black basaltic rock and boulders. The exposure is west-southwest; the vegetation open and characterized by *Cereus giganteus, Cercidium microphyllum, Encelia farinosa, Erigonum fasciculatum, Fouquieria splendens, Larrea divaricata, Lippia wrightii, Psilostrophe cooperi, Spaeralcea,* and species of

FIGURE 13.—Burro Creek site, Mohave County, Arizona. Desertscrub, Sonoran Desert. Lower Sonoran.—A. Southwest-facing slope at the south side of Burro Creek. Substratum littered with black volcanic rocks and boulders. Upper stratum dominated by *Cercidium microphyllum* and *Cereus giganteus*. Plants #0-172, 204, and 203 were sampled during the monitoring period.—B. Sampling site south of Burro Creek. Understory contains *Psilostrophe*, *Lippia*, *Eriogonum*, *Lycium*, and grasses. In additon to *Cereus*, other common cacti include *Echinocactus*, *Echinocereus*, *Mammallaria*, and *Opuntia*. Photos taken 18 June 1968.

Lycium (Fig. 13). The sparse understory has several cactus species (*Echinocactus acanthodes, Echinocereus engelmannii, Opuntia acanthocarpa, O. leptocaulis,* and *O. phaecantha*).

The south of Wikieup site (616 m) is on the south-facing slope of one of the rolling hills bordering Gray Wash (Fig. 14). The vegetation pattern here is similar to that near Burro Creek, and although common in southern Arizona it is limited in extent in Mohave County to the southwestern corner (Humphrey, 1964). Here there is excellent sahuaro reproduction in an area characterized by open vegetation. The sahuaros are not found in the bottoms of the washes, but, as usual, are found on the south-facing slopes with *Atriplex canescens, Calliandra eriophylla, Cercidium microphyllum, Condalia lycioides, Chorizanthe rigida, Echinocereus engelmannii, Eriogonum fasciculatum, Fouquieria splendens, Franseria dumosa, Hymenoclea monogyra, Opuntia acanthocarpa, O. leptocaulis, Prosopis juliflora, Psilostrophe cooperi,* and grasses.

The site farthest north, north of Wikieup (725 m), is also located on a south-facing slope in an area of rolling hills (Fig. 15). These hills run at right angles to the southward-flowing Big Sandy River. The hills here are closer together than at the south of Wikieup site with the washes being correspondingly narrower and the hillsides steeper (Fig. 15). Again the sahuaro is one of the dominant plants along with *Cercidium microphyllum, Fouquieria splendens,* and *Prosopis juliflora.* Other abundant species include *Acacia greggii, Encelia farinosa, Ephedra, Eriogonum fasciculatum, Franseria dumosa, Gutierrezia sarothrae, Hymenoclea monogyra, Juniperus monosperma, Larrea divaricata, Lippia wrightii, Lycium, Opuntia acanthocarpa, O. basilaris, O. leptocaulis, Prosopis juliflora,* and *Psilostrophe cooperi.* The shrub cover is greater on the floor of the washes (30–75%) than on the slopes (15–40%) where the arborescent species are mainly confined (Fig. 15).

The fauna of the region is heterogenous and does not lend itself readily to a simple listing of Sonoran Desert or Mohave Desert forms. Most of the mammals are found in both deserts (Hagmeier & Stults, 1964; Hagmeier, 1966; Hall & Kelson, 1959; Cockrum, 1960). Those approaching here the edge of their geographic distribution are Sonoran elements, *e.g., Citellus harrisi* (Harris Antelope Squirrel) and species of *Perognathus* (Pocket Mice).

The herpetofauna also shares its specific distribution with both deserts (Stebbins & Miller, 1964; Stebbins, 1954; 1966). Again the forms nearing the limits of distribution are mainly Sonoran, *e.g., Sceloporus clarki* (Sonora Spiny Lizard), *Micruroides euryxanthus* (Arizona Coral Snake), and *Heloderma suspectum* (Gila Monster).

The avifauna is the most diverse of the vertebrate groups in this area. The absence of extensive arboreal vegetation in the Mohave Desert limits the distribution of species utilizing tree-form plants. Within the Picidae, *Centurus uropygailis* (Gila Woodpecker) and *Colaptes auratus* (Gilded Flicker) are not found in the Mohave Desert because of their dependence on thick-trunked arboreal species for nesting sites, which are supplied by the sahuaro in the Sonoran Desert. *Dendrocopos scalaris* (Cactus Woodpecker), found nesting in the Sonoran Desert

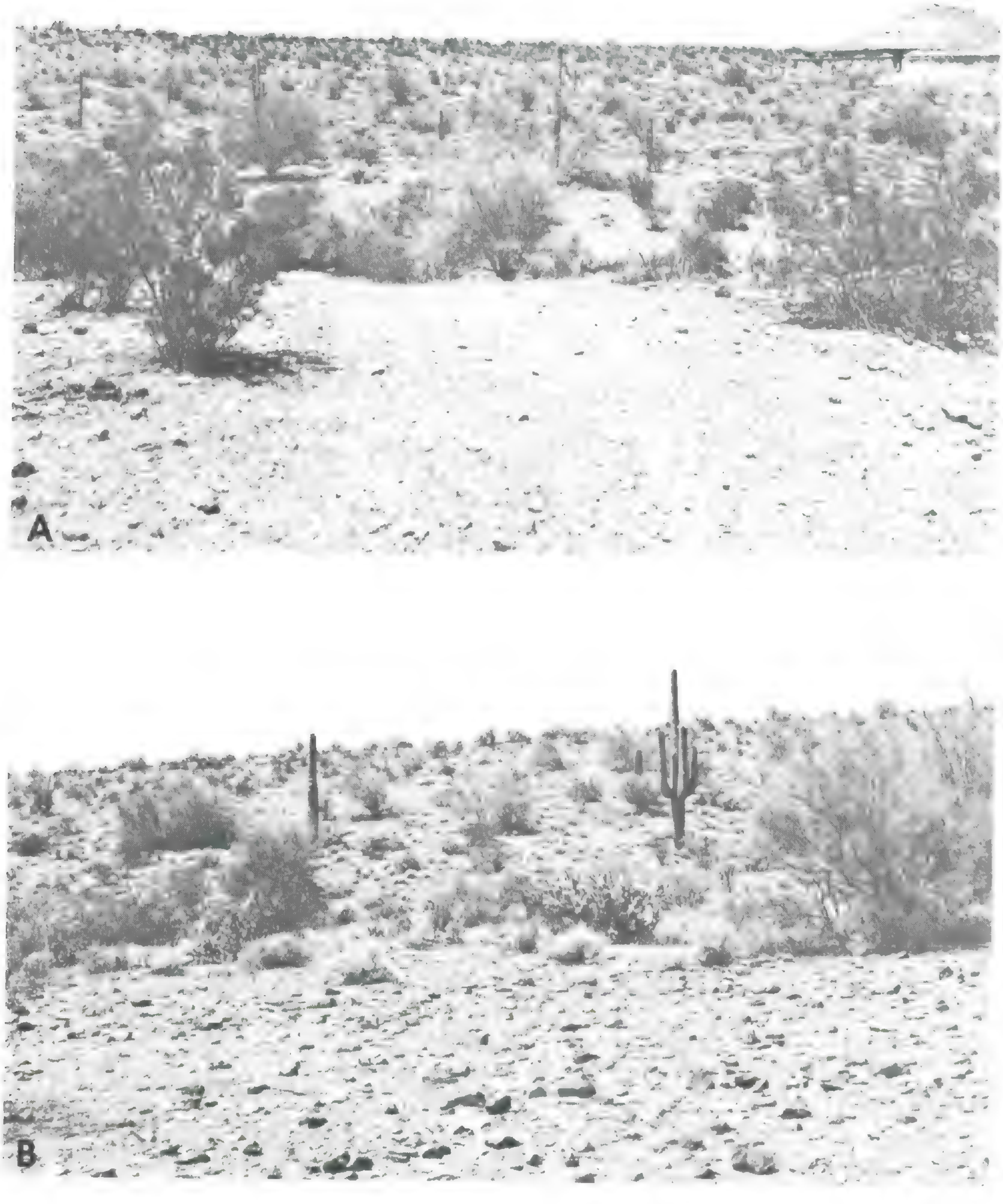

FIGURE 14.—South of Wikieup site, Mohave County, Arizona. Desertscrub, Sonoran Desert. Lower Sonoran.—A. Sahuaros on south-facing rolling hills bordering Gray Wash. Drainage from this site is into the Big Sandy River to the west (left). *Larrea* in foreground. The numbered sahuaros (#0-136, 0-137, 0-135, and 0-173; left to right) were sampled during the monitoring period.—B. Open vegetation; upper stratum dominated by *Cereus giganteus* and *Cercidium microphyllum*, understory dominated by *Franseria dumosa* and *Krameria parvifolia*. Photos taken 18 June 1968.

TABLE 11. Mean values of the osmotic concentration for south and north sides of sahuaros in populations at the five monitoring sites in northern Arizona. September 1966, October 1966, and January 1967.

Site	September		October		January	
	South (mOsm)	North (mOsm)	South (mOsm)	North (mOsm)	South (mOsm)	North (mOsm)
Santa Maria River	—	—	270.8	237.0	187.0	198.8
Juniper Site	313.8	327.6	267.8	261.6	200.1	204.7
Burro Creek	—	—	257.4	285.9	218.0	197.1
South of Wikieup	—	—	235.5	240.7	211.5	209.2
North of Wikieup	244.7	224.3	224.6	219.6	189.3	212.0

in *Agave* stalks and cholla stems, is found in association with *Yucca brevifolia* in the Mohave Desert.

In summary, the plant communities associated with the northern geographic limit of the sahuaro have elements from two major North American deserts (Mohave Desert and Sonoran Desert). This gives the vegetation a definite ecotonal nature which is obvious both in the geographic distribution of the species present and the physical structure of the plant community (arborescent and arboreous species, Sonoran Desert; fruticose species, Mohave Desert).

The vertebrate species can not be compared as easily in terms of specific desert affinity since most are found in both the Mohave and Sonoran Deserts. However, the species which do not extend their range a great distance beyond this vegetational ecotone are generally Sonoran Desert forms extending north and northwest as compared to Mohave Desert forms extending south and southwest. Much of this restriction on the Sonoran Desert animals is related to the need of the species such as *Sceloporus clarki* (Sonora Spiny Lizard), *Centurus uropygailis* (Gila Woodpecker), and *Colaptes auratus* (Gilded Flicker) for trees which are not available in the Mohave Desert. The finding of some Sonoran elements advancing into areas of the Mohave Desert, with little flow in the reverse direction, is to be expected. The Mohave Desert is a transitional area (Lowe, 1967*a*). "The Mohave Desert is in fact an area of tansition with extensive mixture of Sonoran and Great Basin faunas" (Miller, 1951). As an area of ecotonal nature, it has an impoverished endemic fauna. Therefore, the fauna at the northern limit of the sahuaro near the northern edge of the Sonoran Desert and the southern edge of the Mohave Desert would naturally emphasize Sonoran elements which are entering the ecotone, with some effect of Mohave endemics and little Great Basin influence.

Soil. The sites located in the drainage of the Santa Maria River and the Big Sandy River are on the weakly to moderately consolidated alluvium of early Quaternary and late Tertiary age, while Burro Creek and Juniper sites are associated with igneous rocks. The Burro Creek site is on a basalt flow of Pleistocene age, while the Juniper site is on a much older igneous instrusion which is chiefly granite (Cooley, 1967; Wilson, 1962).

The soil analyzed from the northern distribution of the sahuaro was collected near the base of the northernmost naturally occurring sahuaro (17.3 miles north of Wikieup Post Office, U. S. Highway 93, Mohave County, Arizona, 933 m).

FIGURE 15.—North of Wikieup site, Mohave County, Arizona. Desertscrub, Sonoran Desert. Lower Sonoran. —A. Sahuaros on south-facing slopes. These hills are steeper than those at the South of Wikieup Site. The Hualpai Mountains are in the background (west), and the drainage in the foreground continues into the Big Sandy River to the east. Dominant species in the foreground are *Prosopis juliflora, Larrea divaricata, Lycium, Franseria dumosa, Hymenoclea monogyra,* and *Opuntia leptocaulis.* —B. Numbered sahuaros (#0 199, 0 200, and 0-227; left to right) on a south-facing hillside. In the wash the dominant species are *Franseria dumosa* and *Psilostrophe cooperi;* and on the slopes *Cereus giganteus, Cercidium microphyllum, Larrea divaricata,* and *Encelia farinosa* are dominant.

The substratum and plant community here are similar to those at the Santa Maria River site and the substrata and plant communities of the sites south and north of Wikieup.

Mechanical analysis of the surface soil places it in the sandy loam textural class, while the soil at 15 cm is a loamy sand (Table 1). The amounts of sand, silt and clay are intermediate between the site samples examined in southern Sonora and southern Arizona.

Even though the particle size of the soil at the northern end of the distribution of the sahuaro is intermediate, the maximum water-holding capacity is the lowest of any of soils from the sites examined (Table 2). However, with increasing pressure the moisture constants for the northern Arizona soil approach those for the soil in the Tucson region. The soils from the localities in northern Arizona have greater moisture-holding capacity (against pressure of 15 bars 14.8 atmospheres) than soils tested from southern Arizona (Saguaro National Monument, Tucson Mountains), but are exceeded in capacity by the soils from southern Sonora (Table 2).

Both the wet and dry soil from northern Arizona has the lightest color and greatest reflectivity of any of the soils examined along the latitudinal transect (Table 3). This is important in considering the energy budget for this community since the open nature of the habitat, coverage equals 15–60%, presents a large radiating and reflecting surface.

The pH of the soil here is similar to that on southern Sonora and higher than that in Saguaro National Monument (Table 4). As a saturated soil paste (surface soil pH = 8.2, 15 cm pH = 8.0) the pH of the soil from Northern Arizona is neutral to slightly alkaline. However, the pH of the soil at both levels is within the range of soil neutrality as a soil-water extract (pH = 7.8).

The buffer capacity of this soil is greatly reduced in comparison to the soil from southern Sonora (Table 5). In addition the organic matter (autoclave extract) of the surface soil is only about one half of that in southern Sonora, and at 15 cm it is less than one third (Table 5). Other factors which effect the buffer capacity of the soil, such as total carbon, total nitrogen, organic carbon, and organic nitrogen, are all reduced as much as 75–80% of the values for the soil from southern Sonora (Table 6). However, the carbonate carbon content at 15 cm is higher in this soil than it is in southern Sonora (Table 6).

OSMOTIC CONCENTRATION

The osmotic pressure of sahuaro tissue fluids was monitored to determine differences in tissue resistance to low temperature, as indicated by higher osmotic concentrations in sahuaros which were normally subjected to lower environmental temperatures. A characteristic that is as fundamental as the osmotic concentration of the plant tissue fluids should be taken into account fully in ecological surveys (Harris & Lawrence, 1916). This was first done by Drabble and Drabble (1907) in England and later by Fitting (1911) in Egypt, who was the first to study extensively osmotic pressure as a plant characteristic ecologically related to environmental conditions (Livingstone, 1911). The first study of this kind in the United

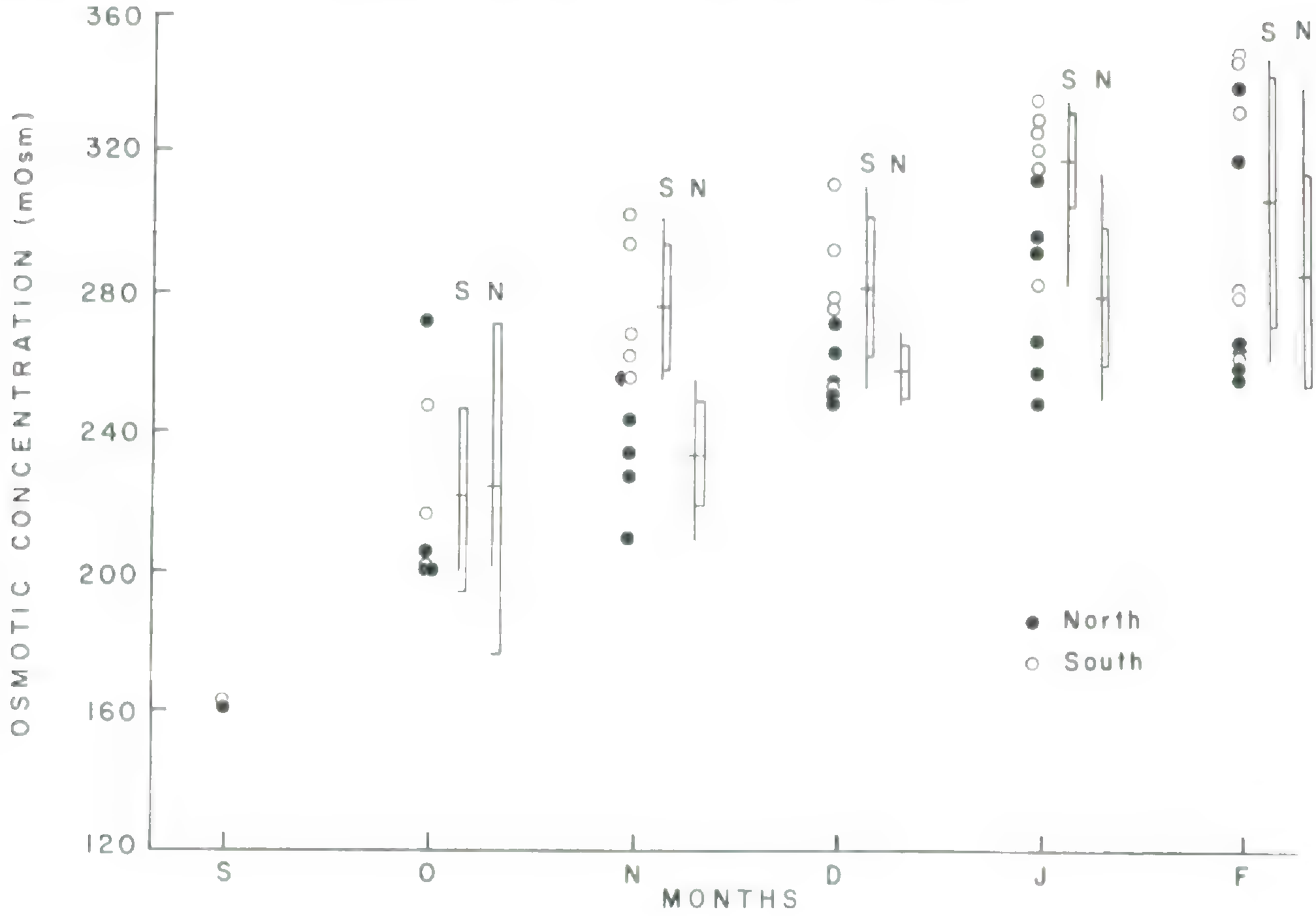

FIGURE 16.—Change in osmotic concentration (mOsm) of sahuaro cortex fluids on Cerro Prieto, Sonora, Mexico, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions of osmotic pressure for each month of the monitoring period for south and north sides in the sahuaro population.

States (Harris, Lawrence & Gortner, 1915) was conducted in part at the Desert Laboratory in Tucson.

Livingstone (1906) said that *Cereus* and other cacti of the desert near Tucson "exhibit osmotic pressures no higher than those commonly found in plants of humid regions. Therefore, for these cacti at least, adaptation to desert conditions is not manifest in increased concentration of the cell sap." MacDougal (1911) expanded this to show that spinose woody plants of the Tucson region have high osmotic pressures and deep root systems which are active most of the year, while cacti have low osmotic pressures and shallow root systems with an ephemeral nature which are activated by the periodic rains. Comparison of the osmotic concentrations of Sonoran Desert cactus species with cacti of the Jamacian "deserts" gives similar values (Harris & Lawrence, 1916).

Even though the osmotic concentration of desert cactus tissue fluids is considerably lower than that of the woody or ligneous desert species, it is subject to change due to variation in environmental conditions, *e.g.*, water deficit (MacDougal & Spalding, 1910). This was shown to exist by MacDougal (1925) and by Walter (1931, 1964). Values cited in the literature for the osmotic pressure of sahuaro tissue fluids are consistent with those obtained in this study (Table 8).

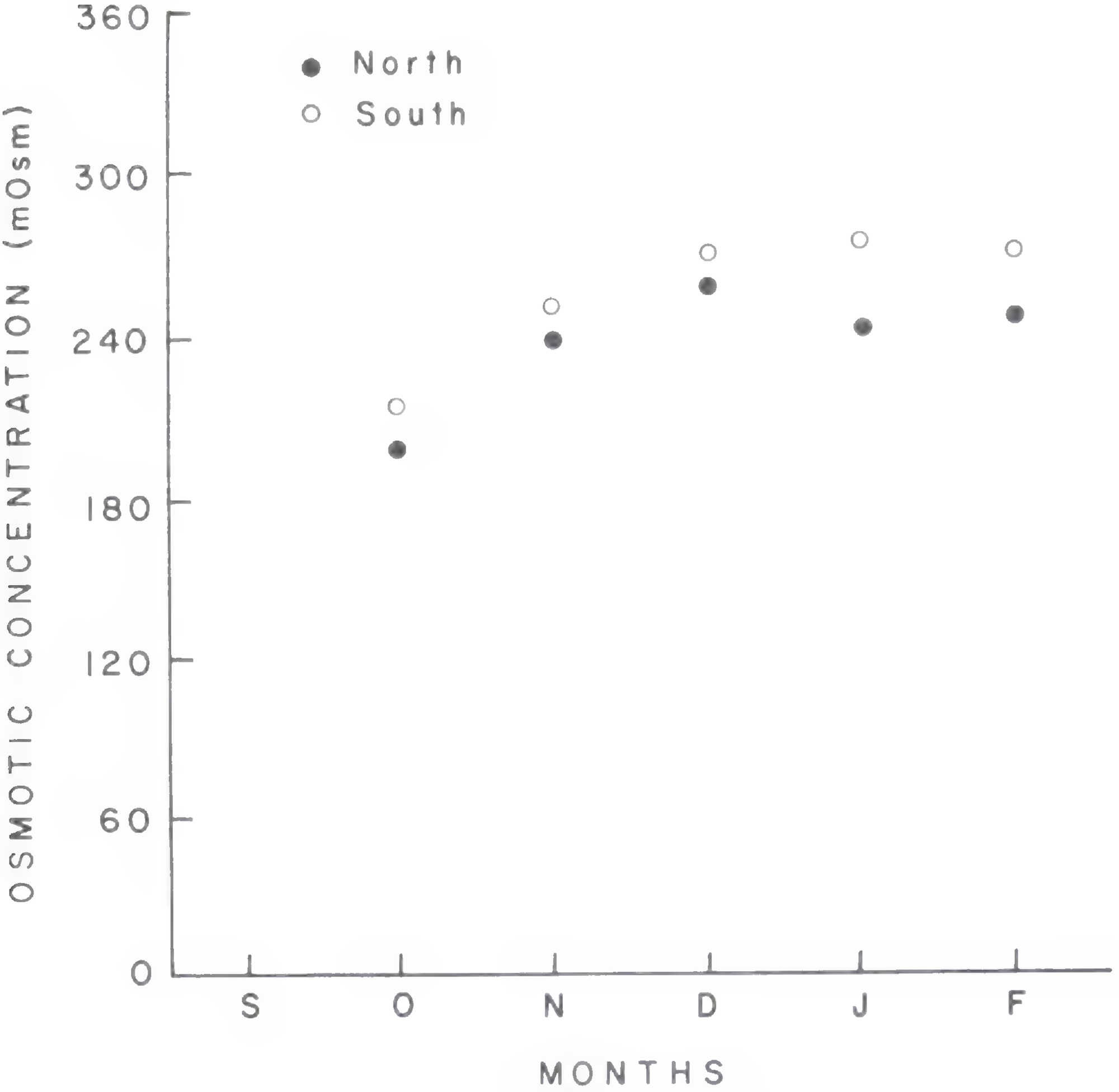

FIGURE 17.—Change in osmotic concentration (mOsm) of cortex tissue fluids of sahuaro #179 on Cerro Prieto, Sonora, Mexico, from October 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

SOUTHERN SONORA

Cerro Prieto. The seasonal change of plant fluid concentration within the sahuaro population at Cerro Prieto (see Habitats) was a steady increase throughout the six-month period of monitoring, summarized in Fig. 16. Eleven sahuaros were sampled a total of 27 times during the period of study. Samples were taken from the north and south sides of the tree with one exception (Figs. 16–17). The exceedingly low initial osmotic concentration values can be attributed to the extremely heavy rains which fell during the late summer months (Table 24). During the entire six months of monitoring, only two days had any appreciable rain (Table 14). Thus the almost complete lack of precipitation and relatively high ambient temperatures (Table 18, Fig. 49) placed the sahuaros in a potential water stress condition. The values for each month were successively higher.

FIGURE 18.—Cerro Masiaca, Sonora, Mexico. The sahuaros on the south-facing slope are found in areas of dense thornscrub vegetation, not on the open black volcanic substratum. The open substratum is composed of basaltic boulders with little soil formation taking place and little vegetation. Photo taken 21 September 1966.

This increase became significant ($P < .05$) when comparing samples at two month intervals (October–January). In February the extreme values at the south side were higher than January, but the mean was slightly lower. The osmotic concentration on the north side was increased over that for January (Fig. 16).

When sahuaros were in an advanced state of hydration (September and October), there was no significant difference between the concentration on the north and south sides of the plant (Figs. 16, 41; Table 15). This difference was due to the same factors which influence the over-all water relations in the community. Also at this time the plant had the minimum freezing-point depression, a minimum resistance to freezing temperatures.

Increasing water stress resulted from net water loss, and this was apparent through increased concentration of plant fluids (Fig. 16). The south side of the plant lost more water due to higher tissue temperatures (Lowe, 1966) and increased transpiration (MacDougal, 1911), even though there are fewer stomates on the south side of the plant (Soule, unpublished data). The combination of these aspects of environmental stress resulted in greater water loss on the south than for the north side of the plants. This difference in concentration between the

TABLE 12. Maximum and minimum temperatures at the North of Wikieup Site and the Juniper Site in northern Arizona. December 1966 February 1967.

	North of Wikieup		Juniper Site	
	Maximum	Minimum	Maximum	Minimum
December 1966	33.9° C (93° F)	+2.2° C (36° F)	26.7° C (80° F)	−1.1° C (30° F)
January 1967	27.2° C (81° F)	3.3° C (26° F)	21.1° C (70° F)	−7.2° C (19° F)
February 1967	30.6° C (87° F)	+0.6° C (33° F)	25.6° C (78° F)	- 4.4° C (34° F)

two sides increased until it became significant ($P < .05$; November) due to the stress, *i.e.*, loss of water, not being reduced.

A single plant reflected the change in osmotic concentration more precisely than the response of the whole population (Fig. 17). For example, plant #179 showed a steady increase in the concentration of the plant fluids from the initial observation until the first major rain of the winter on 31 December before the January monitoring. At this point the plant fluid concentration leveled off, even showing a slight dilution in the value for the north side tissue for January. The leveling of the curve, as the need for water was met, resulted from the heavy rain of 31 December. Plant #179 did not show a significant increase in concentration during the month of February even though there was no rain (Figs. 16–17, 41; Table 15). However, the soil in this area is very high in organic content and water-holding capacity (see Habitats: Southern Sonora, *Soil*). This could supply enough water to meet the requirements of the sahuaro for the next month. The population shows a slight increase in osmotic concentration for February (Fig. 16) showing that in many cases the substratum did not retain enough moisture to supply the increased water requirements of the plant.

Cerro Masiaca. The rocky basalt slopes of Cerro Masiaca mark the southern limit of the sahuaros in this study (see Habitats). From field observation this is their southern geographic limit. There is relatively little soil formation on the hillside, and this is overlain by pieces of broken lava (5 cm to 3 m in diameter). On the more open exposures the sahuaros do not appear on the bare lava; instead they are found in the patches of thornscrub vegetation characteristic of these exposures. These islands of vegetation are dense and accumulate large amounts of litter. The taller sahuaros project above the canopy of the smaller deciduous trees, and they are subjected to massive heat loads due to direct radiation as well as extensive reradiation from the black substratum (Fig. 18).

The high porosity of the basaltic rock limits the water-holding capacity of the substratum on the slope. However, the high organic content of the soil supporting the vegetation increases the water-holding capacity (see Habitats).

Thirty-four samples were taken from 12 adult plants on Cerro Masiaca. Each sample consisted of tissue fluids taken from the north and south sides of the same individual, with one exception. The concentration of plant fluids showed a significant ($P < .05$) seasonal increase on Cerro Masiaca on both the south and north sides of the sahuaros. The low initial values in Fig. 19 are a result of

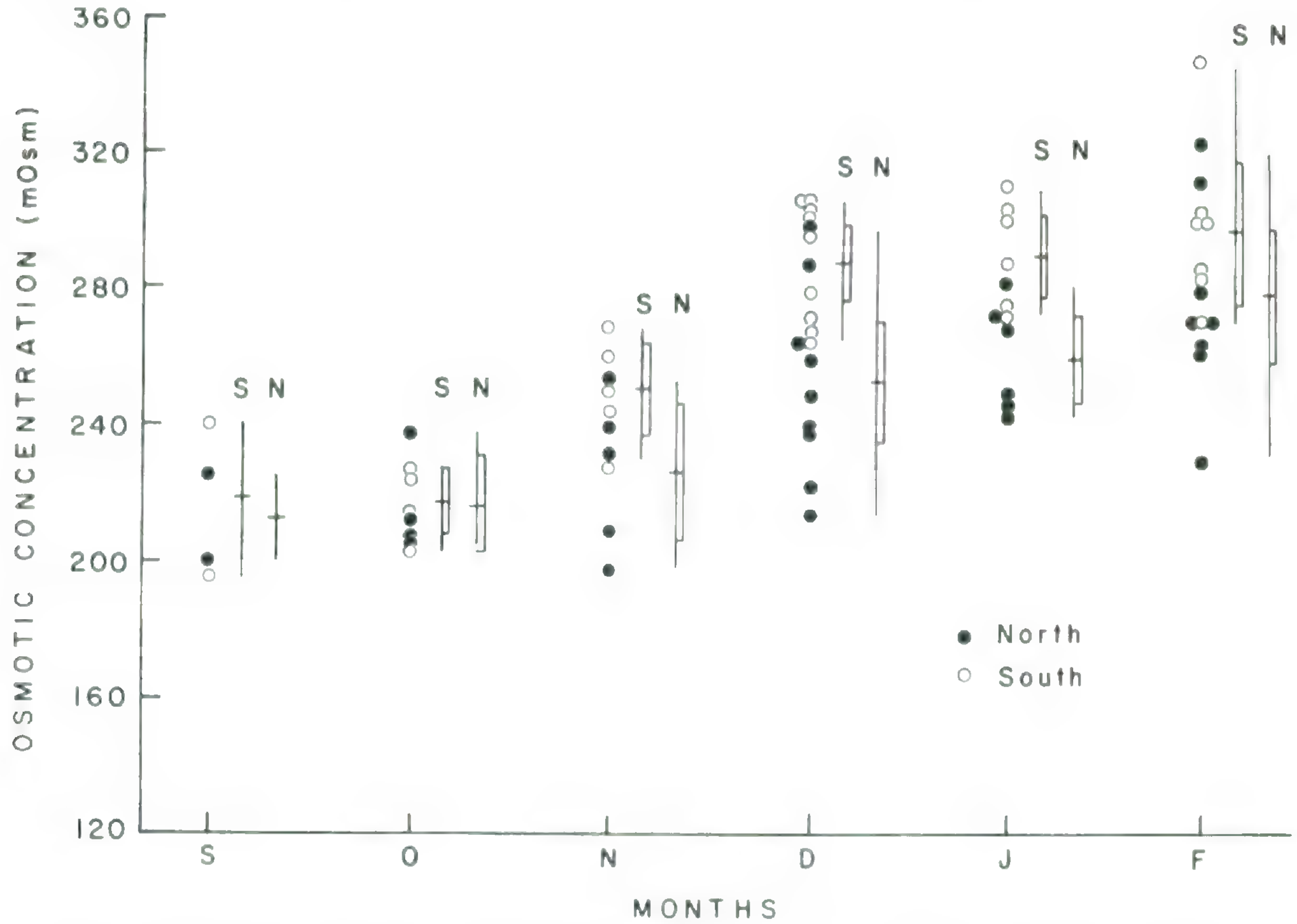

FIGURE 19—Change in osmotic concentration at the population level of sahuaro cortex tissue fluids on Cerro Masiaca, Sonora, Mexico, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions of osmotic pressure (mOsm) for each month of the monitoring period for south and north sides of the sahuaros.

the extremely wet August 1966. This was followed by an extensive drought broken only by the heavy rain of 31 December (Fig. 28, Table 14). With increased stress due to transpiration with no precipitation, the concentration of the plant fluids increased (Fig. 19). Accompanying this significant rise was the change between the north and south sides of the plants. The south side appeared to be more sensitive to changes in concentration. As the drought continued, the difference between the two sides became significant (Fig. 19).

The greater sensitivity of the south sides of the sahuaros was seen in more rapid loss of water on this side (Table 9). This was similar to results reported by MacDougal and Spalding (1910) on examining changes in sahuaro pleat width. The greater water loss can be attributed to the higher tissue temperatures on the south due to greater direct insolation. Again following the brief, but intense, rain of late December (see Climate and Weather) the south sides showed a greater reaction than the north (Fig. 19), again agreeing with the results of MacDougal and Spalding. The mean for the south of the plants leveled off following the rain, indicating substantial water pickup which met the loss due to transpiration. However, the north side continued to increase in concentration but at a reduced rate.

The north-south relationship can be shown more clearly with reference to single plants. Plant #184 from the top of Cerro Masiaca showed a uniform con-

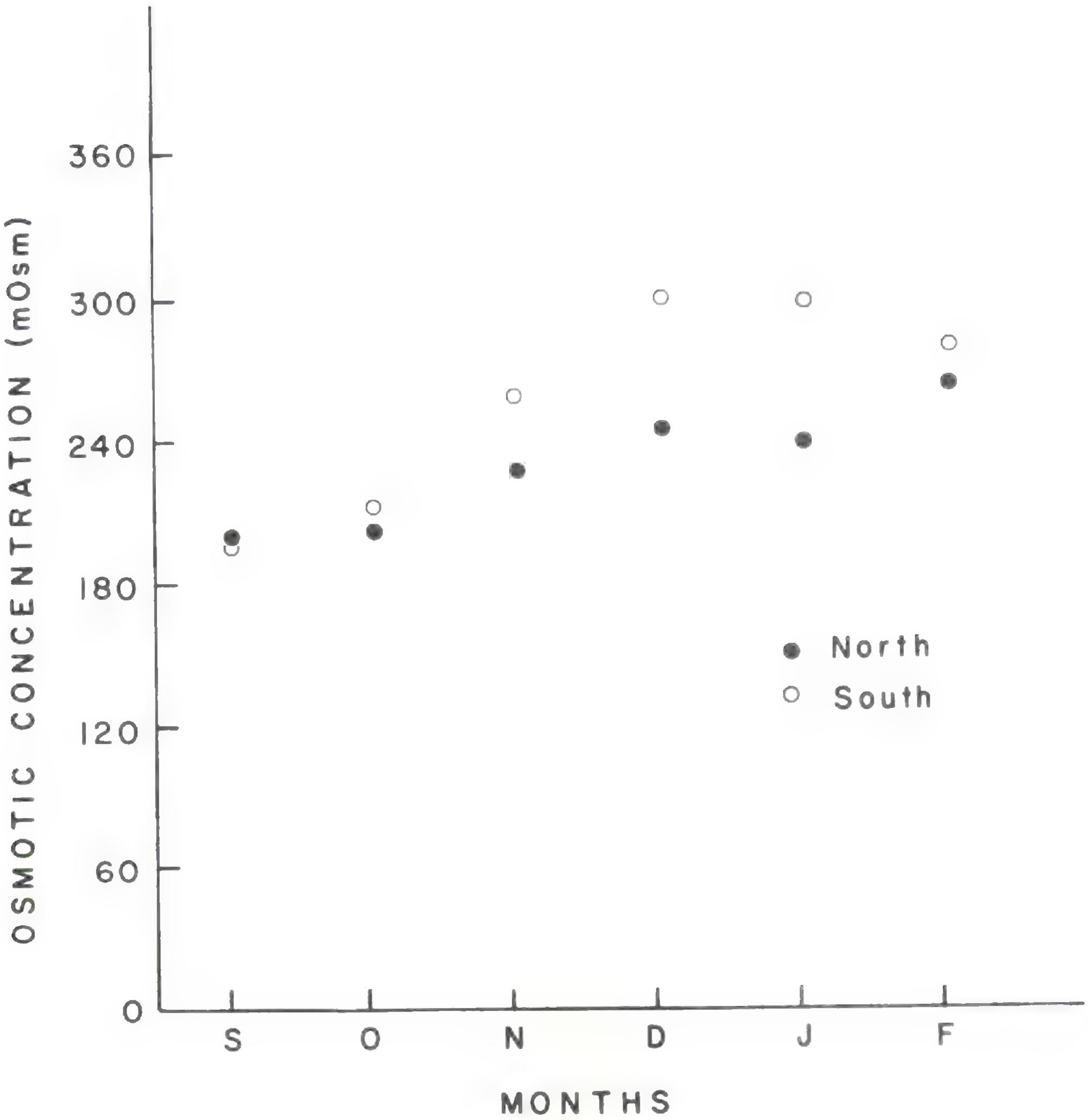

FIGURE 20.—Change in osmotic concentration of sahuaro #184 on Cerro Masiaca from September 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

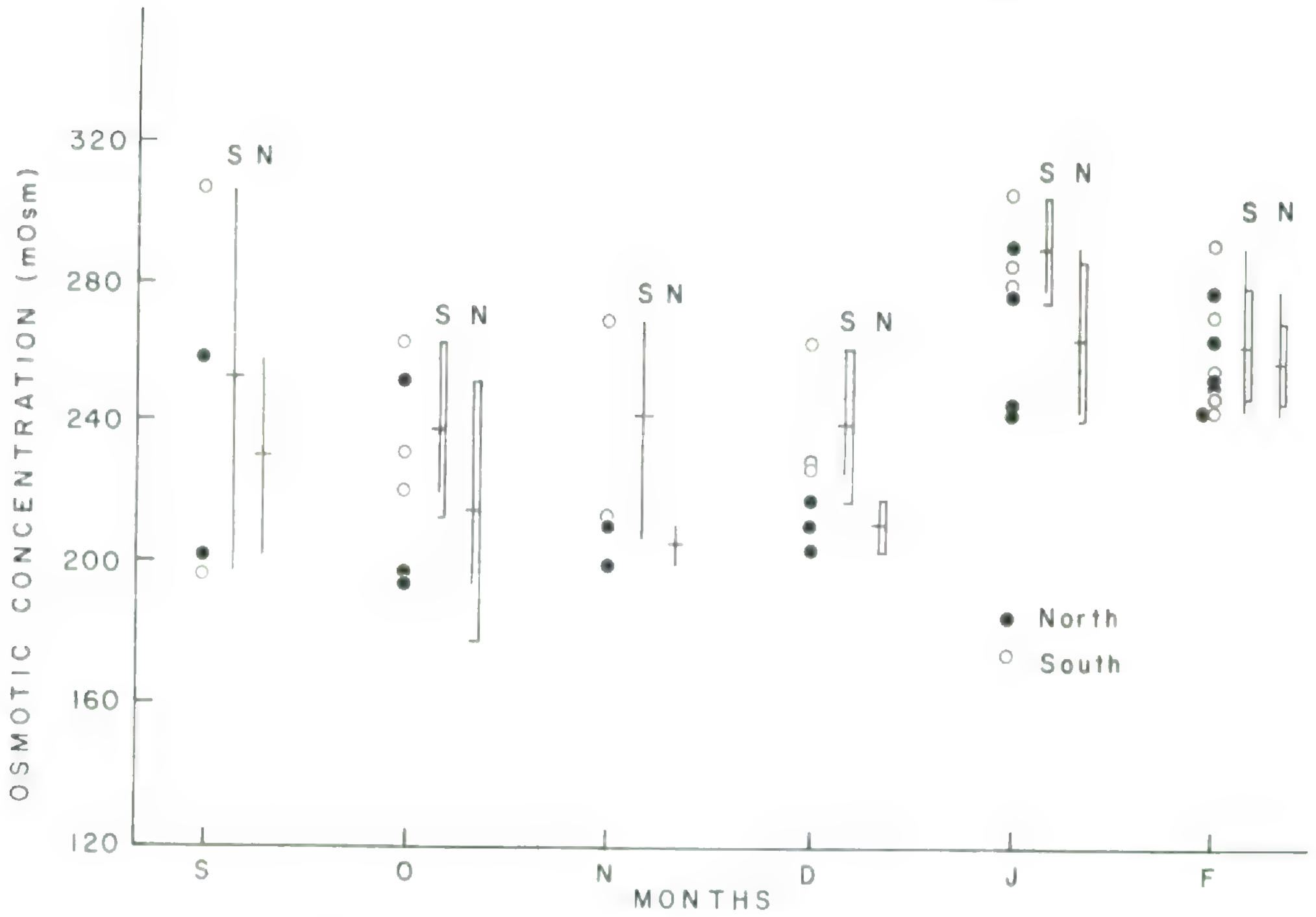

FIGURE 21.—Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids at the population level in Saguaro National Monument Tucson Mountains Section, Pima County, Arizona, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions of osmotic pressure for each month of the monitoring period for south and north sides of the sahuaros.

centration following the late summer rains (198 mOsm, Fig. 20). The plant showed no difference in concentration between the two sides, which is a sign of advanced hydration; the concentration of 198 mOsm suggests the sahuaro was close to full hydration (Table 9). No measurable precipitation occurred between the October and December readings, and the sahuaro was under constant stress due to transpirational water loss. The stress was greater on the south side of the plant than on the north due to the reasons discussed above. This accounted for the significantly higher increase in plant tissue concentration on the south side than on the north in December. The greater rate of increase for the south side as compared to that of the north side of the plant is graphed in Fig. 20. The monthly increase in the differences in the osmotic concentration between the north and south from September through November is three fold. And the difference in December is still twice that of November (Table 10, Fig. 20).

Both north and south sides of plant #184 decreased slightly in concentration in January in response to increased moisture from the rain of late December (Fig. 20). However, the concentration on the south side of plant #184 continued to drop in February suggesting that it is still gaining water, either from the soil or from the north side of the plant. It is possible that the change in concentration in February was due to movement of water from the north to the south since it was observed approximately six weeks after the rain when the south was under higher

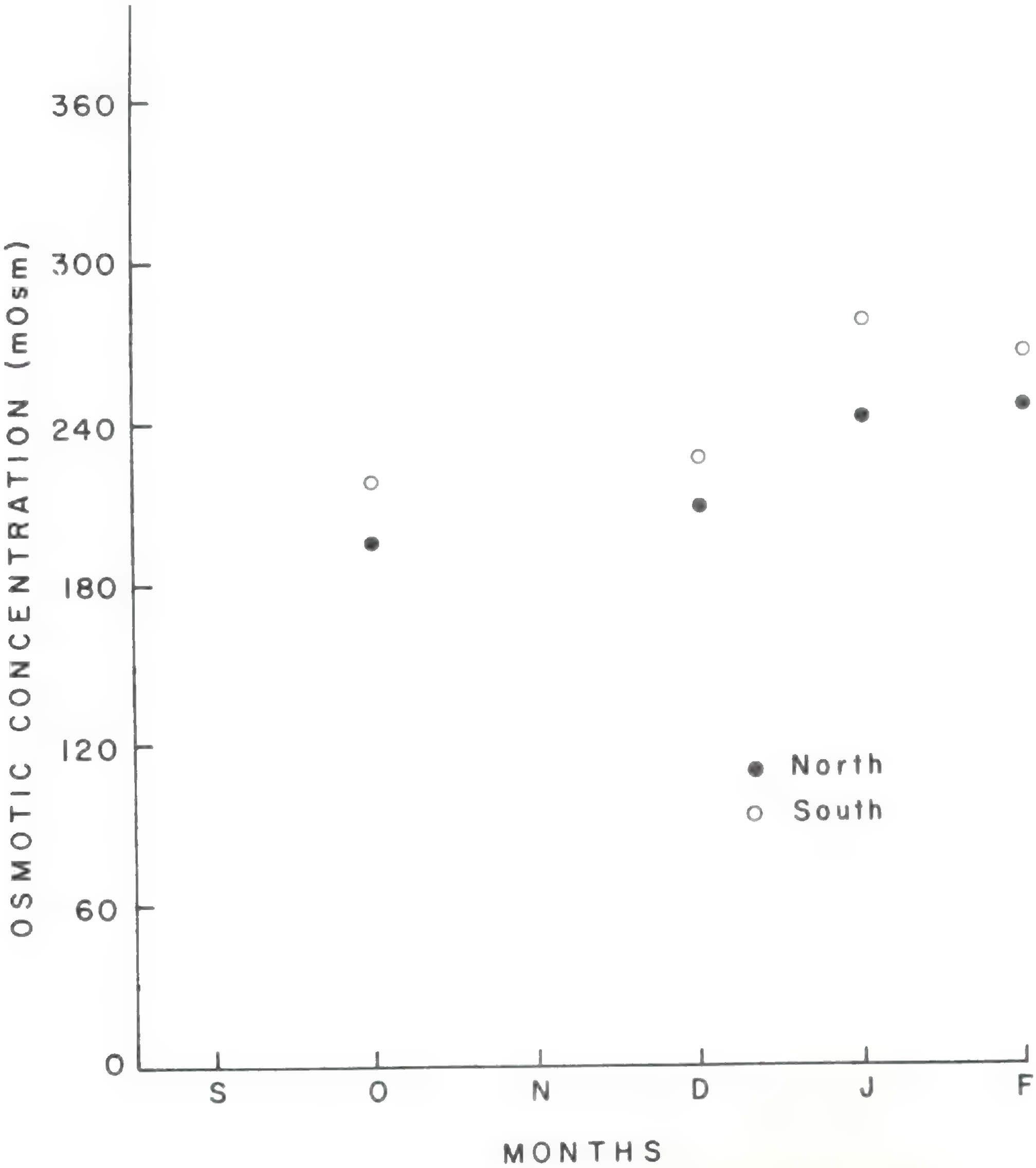

FIGURE 22.—Change in osmotic concentration (mOsm) of sahuaro #0-144 in Saguaro National Monument, Tucson Mountains Section, Pima County, Arizona, from October 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

temperature stress and the concentration gradient was still to the south from the north.

SOUTHERN ARIZONA

Tucson Mountains (Saguaro National Monument). The initial (September) values for the concentration of plant tissue fluids recorded in the Tucson Mountains at Saguaro National Monument were low (*ca.* 200 mOsm; Fig. 21). These were similar to the readings of a like date at the stations in Mexico. This advanced

TABLE 13. Mechanical analysis of soils from the 817 meter site, 869 meter site and 1067 meter site on the Santa Catalina elevational transect. Soil collected January 1968.

		Per cent composition						
Site	Depth	5 mm	5 mm–3 mm	3 mm–2 mm	2 mm–1 mm	1 mm–0.4 mm	0.4 mm	Total
817	Surface	7.28	5.23	5.68	7.45	12.58	61.78	100.00
meters	8 cm	15.48	8.29	14.63	16.03	18.43	27.13	99.99
	16 cm	20.78	19.77	11.29	18.96	14.43	14.78	100.01
869	Surface	22.93	5.73	10.11	15.18	14.92	31.13	100.00
meters	8 cm	11.73	9.38	15.60	21.00	17.27	25.02	100.00
	16 cm	19.16	10.94	13.89	18.78	14.25	22.98	100.00
1067	Surface	19.73	8.67	12.95	14.96	13.99	29.70	100.00
meters	8 cm	31.09	9.77	13.50	16.18	10.50	18.97	100.01
	16 cm	32.52	10.06	12.93	17.96	11.41	15.12	100.00

state of hydration followed above normal rains and an exceptionally wet early September (see Climate and Weather). However, the seasonal increase following this was not as pronounced here as it was in Mexico; it became significant ($P < .05$) in January. Nine adult plants were sampled 19 times in the Tucson Mountain area of Saguaro National Monument on both north and south sides with one exception.

From September through December no significant change took place on either the south or north sides of the sahuaros. However, the south side maintained a significantly higher concentration than the north during November and December.

In January a significant ($P < .05$) rise in the concentration of plant tissue fluids took place on both sides (Fig. 21). January had more precipitation and lower temperature than the previous month. This rise in concentration was broken in February, a month with less precipitation and increased temperature (Fig. 21). The significant increase in osmotic concentration coupled with more precipitation and lower temperature suggests that the amount of precipitation was not sufficient to meet the demands or that a potential hardiness factor was involved.

The overall seasonal trend at the population level in the Tucson Mountains was one of significant increase of osmotic pressure with reduced precipitation and lower temperatures. However, the degree of increase from September to February was reduced in comparison to that of the Mexican stations (Fig. 43). Greater precipitation and lower environmental temperatures together are contributing factors in this difference.

The south sides of the plants showed a more sensitive response to the environmental conditions than did the north. During the period of maximum observed hydration (September) there was no significant difference ($P > .05$) in the concentration of the two sides (Fig. 21, Table 15). With increasing water stress the concentration of the south side increased. This was due in part to higher tissue temperature and greater subsequent water losses due to transpiration.

The individual representative plant, #0-144, from the Tucson Mountains (Saguaro National Monument) showed a response similar to that of the one described for the population (Fig. 22). This was a slight increase in the con-

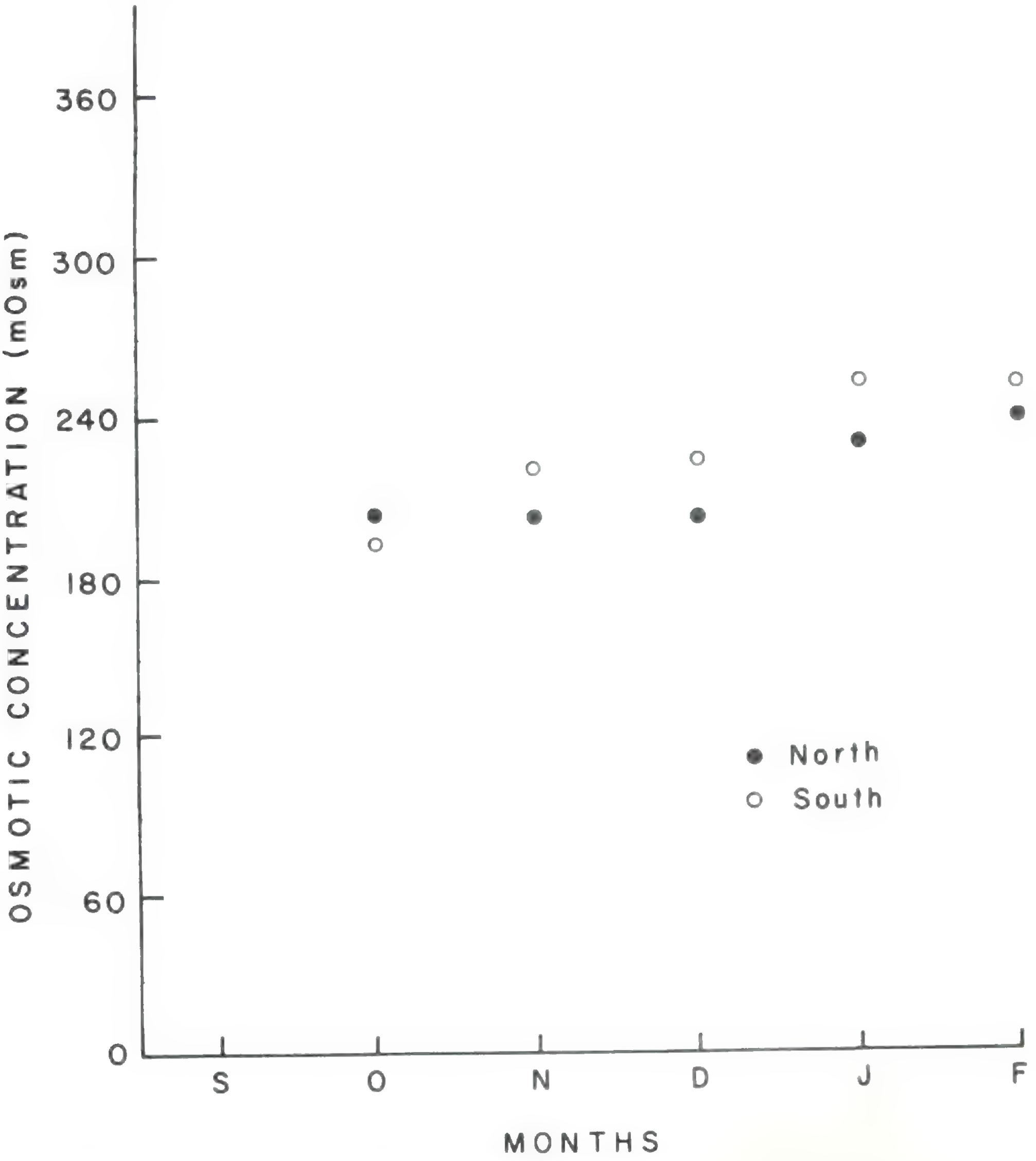

FIGURE 23.—Change in osmotic concentration of sahuaro #0-142 at the Gate's Pass monitoring site in the Tucson Mountains, Pima County, Arizona, from October 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

centration of the plant tissue fluids from October to December, and a sharp rise in January. It should be noted that the lowest environmental temperatures of the season occurred during this period (see Climate and Weather). The following month, February, the concentration of the plant tissue fluids decreased on the south side of plant #0-144 (Fig. 22). This was not in response to the increased precipitation, but possibly reflects carry over of hydration from January or a genetically controlled hardiness factor.

Tucson Mountains (Gate's Pass). The concentrations of plant tissue fluids for the sahuaros in the Gate's Pass area of the Tucson Mountains were similar to

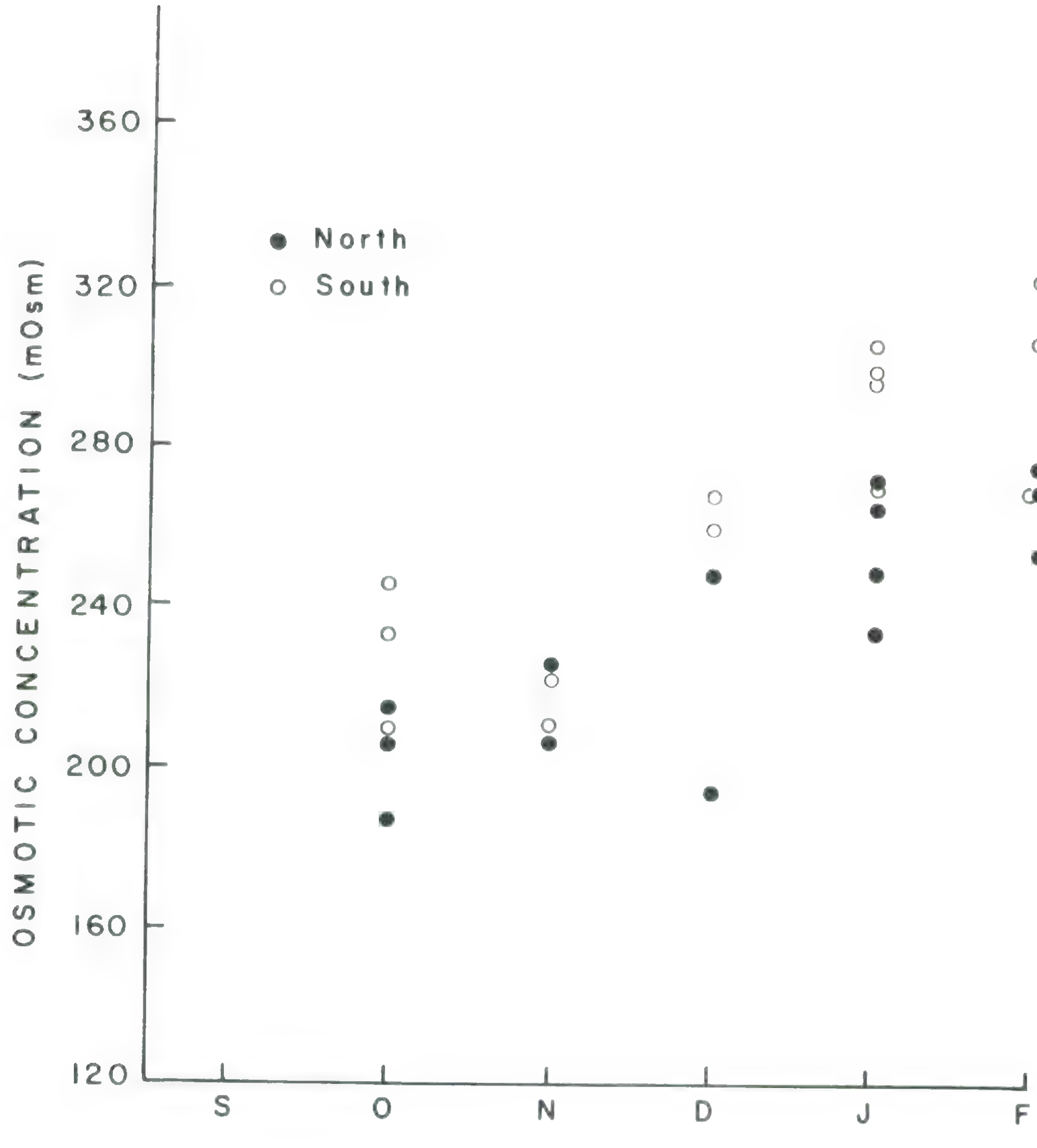

FIGURE 24.—Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids of plants at the Santa Catalina foothills monitoring site, Pima County, Arizona, from October 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

those for Saguaro National Monument in the Tucson Mountains both in magnitude and direction of change. Eight samples were taken from two sahuaros during the monitoring period of October 1966 through February 1967. The October values (Fig. 23) represent samples taken on different dates.

Starting at a relatively dilute point (*ca.* 210 mOsm), plant #0-142 increased in concentration of tissue fluids until the concentration leveled off at *ca.* 245 mOsm (Fig. 23). This reflects the continued increase in osmotic pressure presumably through the loss of water due to transpiration. Even though this loss was modified during the period of lowest environmental temperatures, the net loss is still represented in these values.

Santa Catalina Foothills (*bajada*). This site is on the rocky bajada on the south side of the Santa Catalina Mountains. In general aspect, the habitat is similar to some of those on the west side of the Tucson Mountains, *e.g.*, in and near the Saguaro National Monument area (see Habitats).

The sahuaros sampled at this site showed a significant ($P < .05$) increase in concentration of tissue fluids throughout the monitoring period (Fig. 24). Fourteen samples were taken from four large plants and showed a range in variation from 188 mOsm (north side, October) to 322 mOsm (south side, February).

From the initial sampling (October mean = 226 mOsm) to the final sampling (February mean = 300 mOsm), the south sides of the plants had a higher concentration of tissue fluids than did the north (October mean = 203 mOsm; February mean = 267.5 mOsm) with the exception of November (Fig. 24). The drop in concentration of the tissue fluids on the south sides of the sahuaros in November (Fig. 24) matches the drop shown by the north sides of the plants during the same month at Saguaro National Monument (Fig. 21).

The difference in osmotic pressure between the north and south sides of the sahuaros is graphed in Fig. 25 (plant #0-147). Again, with minimal precipitation the concentration of the plant tissue fluids is higher on the south side than it is on the north. The rise seen throughout the period of observation, on the Catalina bajada from October 1966 through February 1967, indicates that water loss exceeded gain in this sahuaro as in the population.

The drop of concentration on the south sides of the sahuaros which took place in the Tucson Mountains between January and February did not take place on the Catalina bajada.

Northern Arizona

Santa Maria River. Nine samples were taken from three large plants at this site in the northern part of the range of the sahuaro cactus. The data show a significant ($P < .05$) decrease in concentration of plant fluids during the period of monitoring from a high of 292 mOsm in October to a low of 183 mOsm in January (Fig. 26). The initial high values correspond to the extremely dry summer (see Climate and Weather). The concentration of the sahuaro fluids decreased steadily with the onset of the early winter rains. The months from September through December had more rain than normal (Fig. 51). December was the wettest month of the monitoring period, and the following reading (January) was the lowest with a mean of about 195 mOsm for the population sampled (Fig.

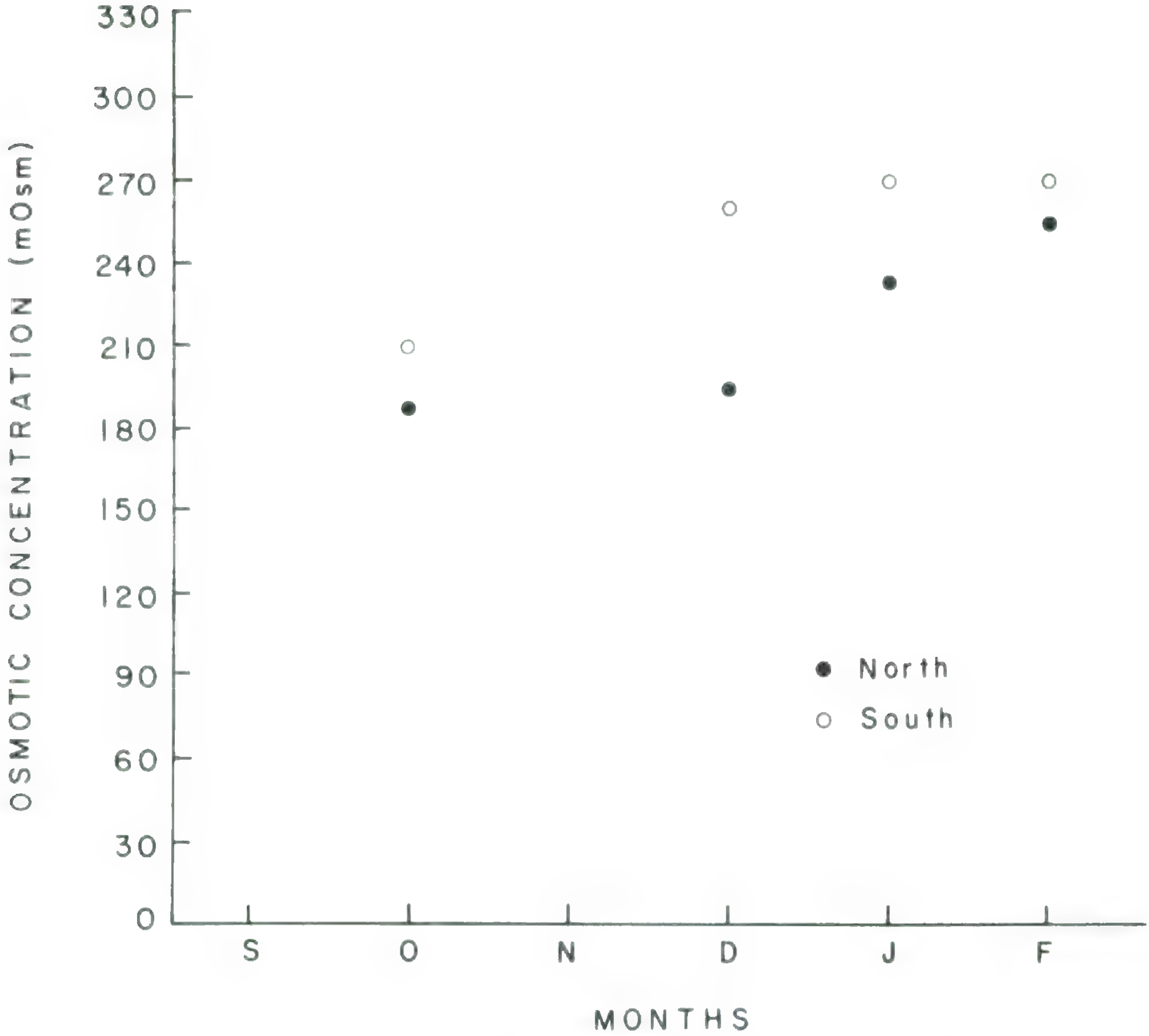

FIGURE 25.—Change in osmotic concentration (mOsm) of sahuaro #0-147 at Santa Catalina foothills monitoring site, Pima County, Arizona, from October 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

26). The rain fell off sharply in January and February. The February reading showed a significant ($P < .05$) increase in concentration with a maximum difference of 75 mOsm between this month and the previous one (Fig. 26). The increases on both the south and north sides were significantly higher than the values for the previous month.

The decrease paralleled the increasing low temperatures with the lowest concentration of plant fluids coinciding with the lowest seasonal temperatures. This is to be expected if the sahuaros take up water supplied by the winter precipitation. This confirms the findings of Steenbergh and Lowe (1969) for winter and Hastings (1959) for summer, that sahuaros in the Tucson region pick up water as a result of both winter and summer rains, but grow only during the warm season.

The increasing values at the stations to the south paralled the lack of precipitation following an extremely wet summer. In northern Arizona after an extremely dry summer (see Climate and Weather), the change in plant tissue

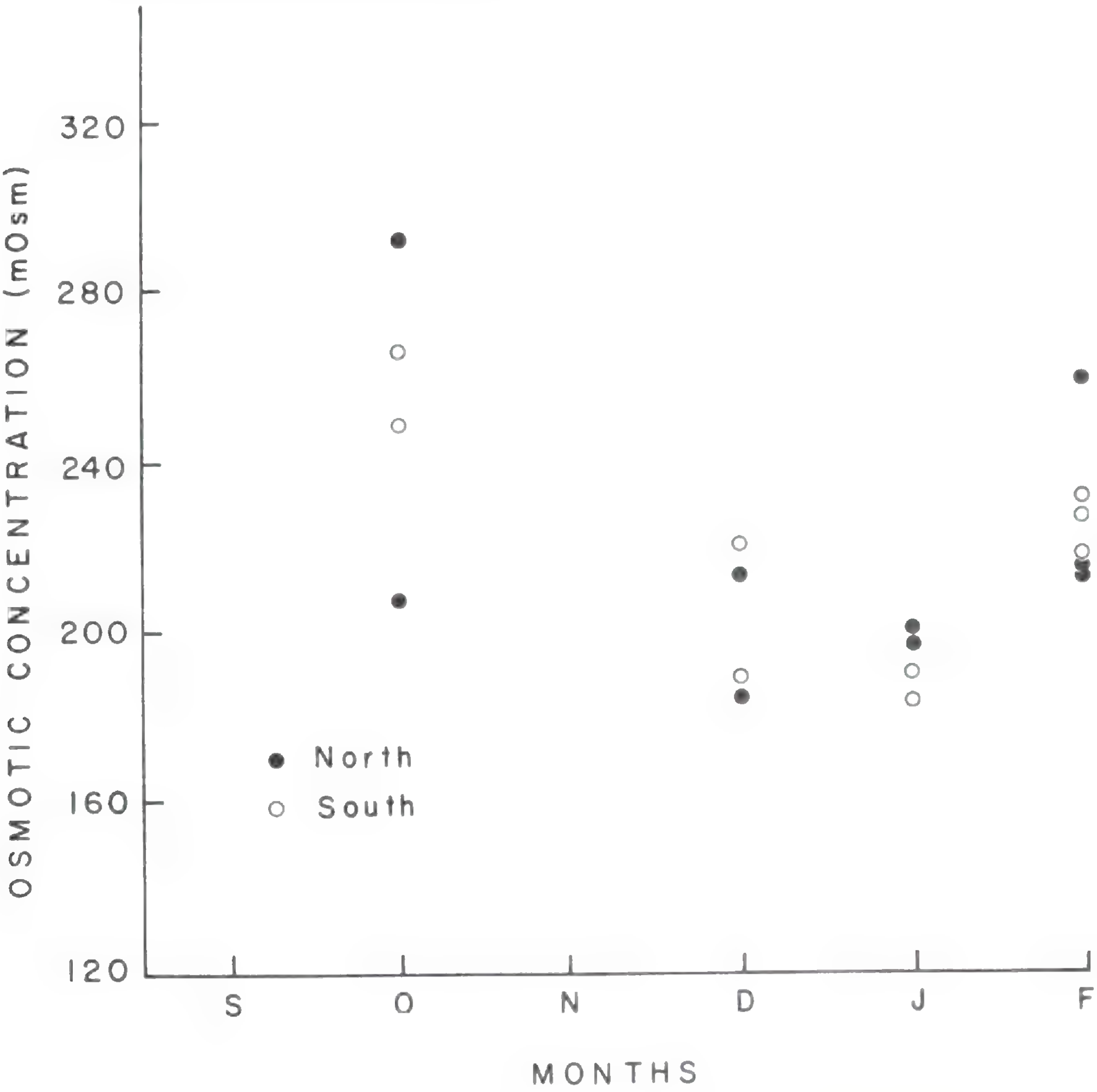

FIGURE 26.—Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids for plants at the Santa Maria River monitoring site, Yavapai County, Arizona, from October 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

osmotic concentration responded to increasing seasonal precipitation rather than decreasing seasonal temperature.

In comparison with the stations in southern Sonora and on the Tuscon bajadas, the differences in concentration between the north and south sides of the plants were not significant for northern Arizona ($P > .05$; Table 15). At the Santa Maria River site the values for the south side tissue were not significantly higher than those of the north (5 mOsm) during the period of hydration. However, at the point of minimum resistance to freezing (maximum hydration), the value for the north side was significantly higher ($P < .05$; Fig. 26). During the following month (February) the mean for the south sides was not significantly different (224 mOsm) than that of the north (228 mOsm), but this was influenced by a single high north value (Fig. 26). However, within the total population sampled

TABLE 14. Effective rainfall between sampling dates (September 1966–February 1967) and total precipitation from June 1966 May 1967 for southern Sonora (Navojoa, Sonora, Mexico), southern Arizona (Tucson International Airport, Pima County, Arizona), and northern Arizona (Wikieup, Mohave County, Arizona).

Site and Date	Total precipitation (inches)	Number of days of measureable precipitation	Number of days with precipitation of 0.1 or more inches	Number of days with precipitation of 0.15 or more inches	Number of days with precipitation of 0.2 or more inches
Southern Sonora					
14 Aug.–21 Sept.	4.87	14	10	10	8
22 Sept.–14 Oct.[a]	1.50	2	1	1	1
15 Oct. 11 Nov.	0.0	0	0	0	0
12 Nov. 16 Dec.	0.0	0	0	0	0
17 Dec.–24 Jan.[b]	0.59	2	1	1	1
25 Jan.–25 Feb.[c]	0.03	1	0	0	0
Southern Arizona					
12 Aug.–20 Sept.	3.38	13	8	6	6
21 Sept.–20 Oct.	0.47	5	2	1	1
21 Oct.–15 Nov.	0.06	1	0	0	0
16 Nov.–18 Dec.	0.01	1	0	0	0
19 Dec.–29 Jan.[d]	0.22	2	1	1	1
30 Jan.–10 Feb.	0.0	0	0	0	0
Northern Arizona					
15 Aug.–24 Sept.[e]	1.23	2	2	1	1
25 Sept. 16 Oct.[f]	0.84	3	2	2	2
17 Oct.–13 Nov.[g]	1.02	1	1	1	1
14 Nov.–19 Dec.[h]	1.08	4	4	4	4
20 Dec.–13 Jan.	0.10	1	1	0	0
14 Jan. 18 Feb.[i]	0.45	1	1	1	1

[a] 1.50 on Sept. 29
[b] 0.99 on Dec. 31
[c] 0.03 on Feb. 19
[d] 0.04 on Jan. 23
[e] 1.10 on Sept. 19
[f] 0.77 on Oct. 4 and 5
[g] 1.02 on Nov. 9
[h] 1.80 on Dec. 4-7
[i] 0.45 on Jan. 24

in northern Arizona, the concentrations on the south sides were significantly higher than those of the north (Table 9). Thus with the reduction in precipitation in January and February, the concentration of sahuaro cortex fluids rose significantly on both the north and south sides.

A clearer picture of the water relations on the north and south sides of the sahuaro is graphed in Fig. 27, which represents a single plant (#186). Following the dry period (summer 1966) the south side of the plant had a higher concentration of tissue fluids than did the north. This was as expected since there is a net water loss under conditions of continued transpiration during hot, dry periods. This difference decreased as water in the form of precipitation became more available. Finally, at the point of maximum hydration (January) the concentration on the south decreased below that on the north (Fig. 27) due either to hydration or a hardiness factor. Following this wet period (October through December), the sahuaro lost water as shown by increase in osmotic pressure of the tissue fluids. This dehydration process resulted in the previous relationship—the south side being more concentrated than the north—being reestablished.

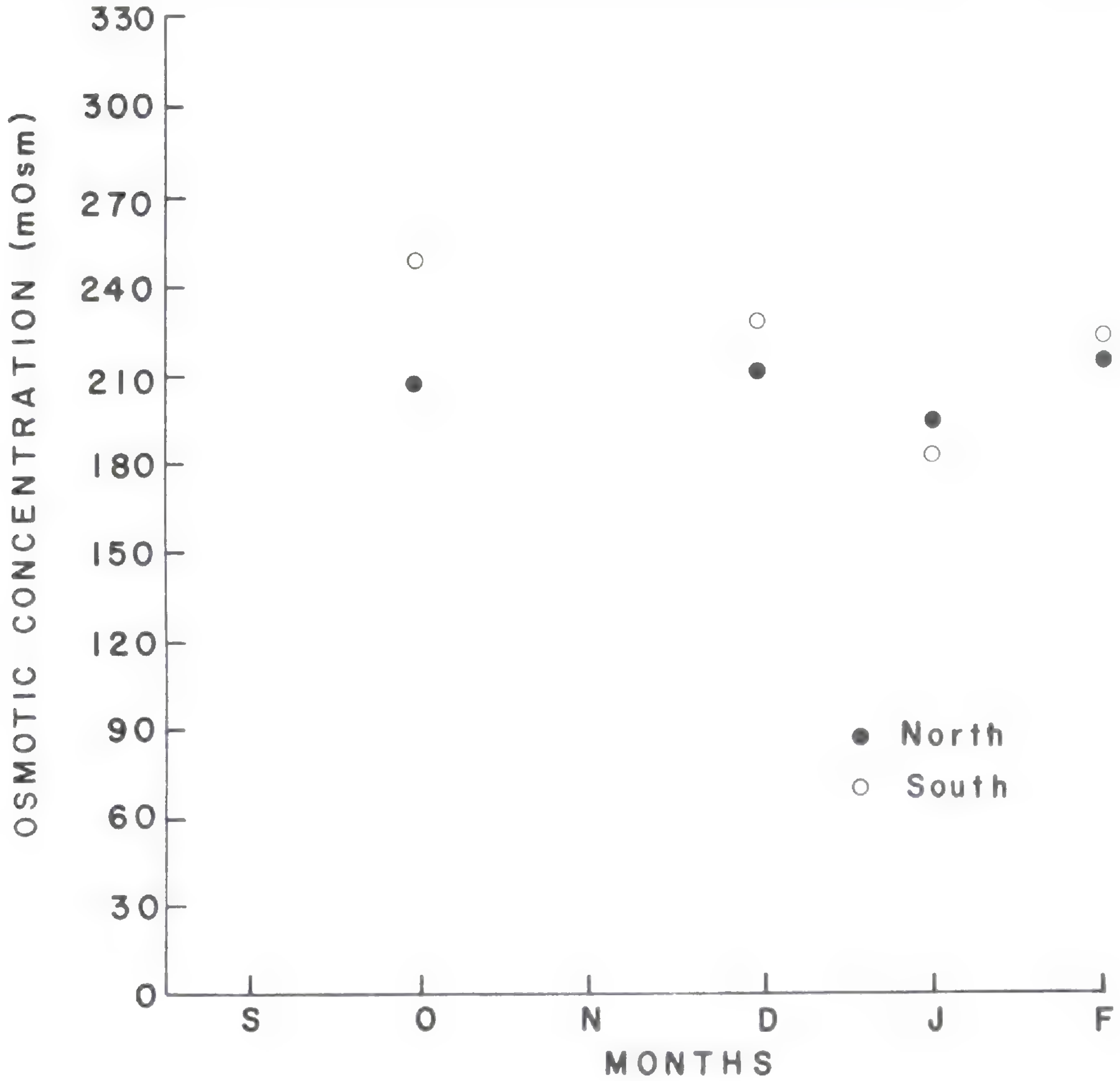

FIGURE 27.—Change in osmotic concentration (mOsm) of sahuaro #186 at Santa Maria River Site, Yavapai County, Arizona, from October 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

The south side of the sahuaro appears to take up moisture more readily than the north side, as indicated by changes in osmotic concentration, in accordance with MacDougal and Spalding (1910). This is due in part to the higher osmotic pressure attained with greater water loss associated with the higher tissue temperatures on the south sides of the sahuaros. However, this increased water content is not maintained indefinitely, and with the subsequent losses the south side once again became more concentrated (February; Fig. 27).

The low point on this curve is potentially limited by two factors: (1) the amount of water available to be taken up by the plant and (2) the maximum hydration of the plant based on physiological and genetic limits. Additional field observation is needed to determine which is limiting under various conditions, but maximum hydration values of 190.3 ±3.3 mOsm (161.7–218.8 mOsm, Table 9) are found throughout the range of the sahuaro. This appears to be an adaptive limit.

TABLE 15. Difference between the concentration of sahuaro cortex fluids on the south and north sides of the plants using the paired comparison test.

Site		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Southern Sonora	P	>.05	>.05	<.001	<.001	<.001	<.001
	t	2.17	0.05	12.08	15.24	14.72	8.10
	N	3	7	10	14	12	13
	d	4.6	0.1	33.1	31.4	34.6	19.3
Southern Arizona	P	>.05	<.001	<.001	<.001	<.001	<.001
	t	4.15	11.03	6.27	11.33	16.65	7.68
	N	3	9	6	8	9	11
	−d	14.8	19.2	21.0	31.6	39.8	21.5
Northern Arizona	P	>.05	>.05	<.01	>.05	>.05	<.001
	t	2.95	0.65	4.24	0.40	0.64	5.63
	N	3	9	9	14	12	18
	−d	9.0	1.8	−11.8	0.8	−1.3	12.4

Juniper Site. This is the highest (991 m) of the northern sample sites and has a plant community more representative of those facing low winter temperatures (see Habitats). The range in concentration of sahuaro fluids was also the greatest of any single site examined in the study—328 mOsm, September to 186 mOsm,

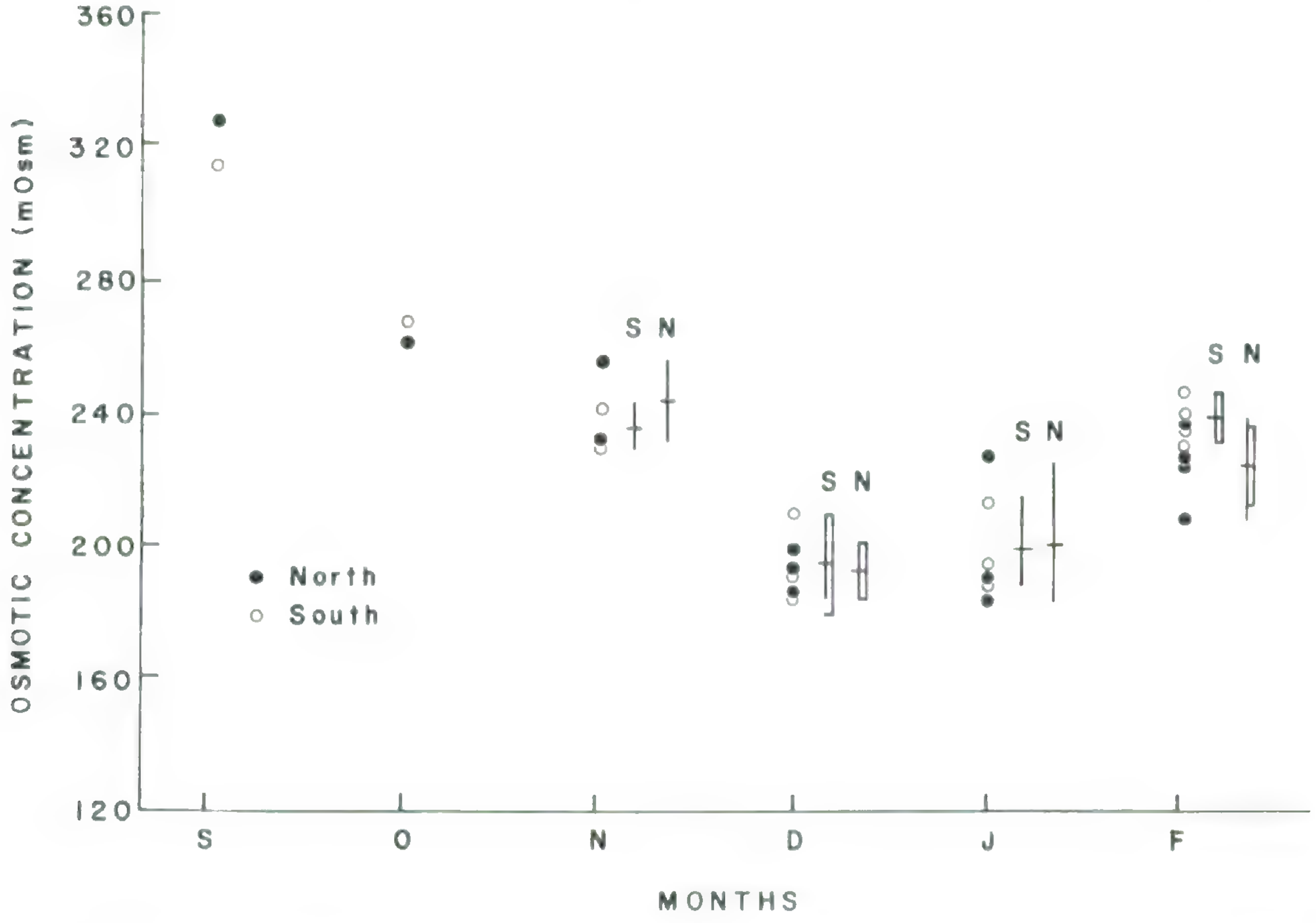

FIGURE 28.—Change in osmotic concentration of sahuaro cortex tissue fluids of plants in the sahuaro population at Juniper Site, Mohave County, Arizona, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions of osmotic pressure for the months of December 1966 and February 1967 for both south and north sides of the sahuaros.

January (Fig. 28). Fourteen samples were taken from five sahuaros from September 1966 through February 1967.

Normally the July-August summer precipitation is the highest two-month period of the year. However, during the summer of 1966 less than five percent of the normal precipitation fell during these months (Fig. 51). Also these two months are normally the hottest of the year, as they were during the summer prior to the period of monitoring (Fig. 48). Thus the plants were placed under water stress by high temperature, low precipitation, and continuing transpirational water loss. This was reflected in the high values of fluid concentration for September (*ca.* 320 mOsm; Fig. 28). This was the reverse of the pattern in southern Sonora and southern Arizona, where the summer rains were heavy and the initial values determined for plant tissue osmotic pressure were low (Figs. 41–42). After the initial readings at this site the change in values for the concentration of plant tissue fluids continued to be the opposite of those of the southern sites. In the south, values increased during each of the fall and winter months, while values here were reduced significantly ($P < .05$) each month until they started to rise toward the end of the monitoring (January and February). The heavier than normal rains which started in September 1966 and continued through the fall and early winter continually diluted the sahuaro tissue fluid osmotic concentration to the low point in December (*ca.* 185 mOsm; Fig. 28). During the period of hydration there was no significant difference in the osmotic concentration of the two sides of the sahuaros (south and north).

In December the rainfall dropped below the seasonal average. The entire January precipitation fell in a single day (0.45 inch, 24 January), and no rain fell in February. The subsequent rise in concentration was significant ($P < .05$) on both the south and north sides of the sahuaros in February being above values for these sides from December and January. With the reduction in available water, it can be assumed that the amount of water gained by the sahuaros soon became less than that being lost by transpiration, and this is graphed as an upswing in plant tissue concentration (Fig. 28).

The north-south relation on a single plant (#202) at this site reflects the trends shown elsewhere (Fig. 29). When under moisture stress, the concentration of the south side is higher. However, when the plant is fully hydrated both sides have approximately the same concentration.

Burro Creek. The substratum of the Burro Creek site resembles the sahuaro localities in southern Sonora, while the sahuaros at the other northern localities grow in substrata similar to that of the bajadas of the mountains near Tucson (see Habitats). At Burro Creek the ground is scattered with basaltic rocks and boulders. Five large plants were sampled, for a total of 11 north-south readings.

Once again the very high initial values can be attributed to the lack of summer rains and the high environmental temperatures to which the plants were subjected (see Climate and Weather). With the onset of the fall and winter rains, the concentration of plant tissue fluids fell from a high of 313 mOsm during the first month of monitoring (October) to a low of 190 mOsm during January (Fig. 30). The decrease was significant ($P < .05$) based on a com-

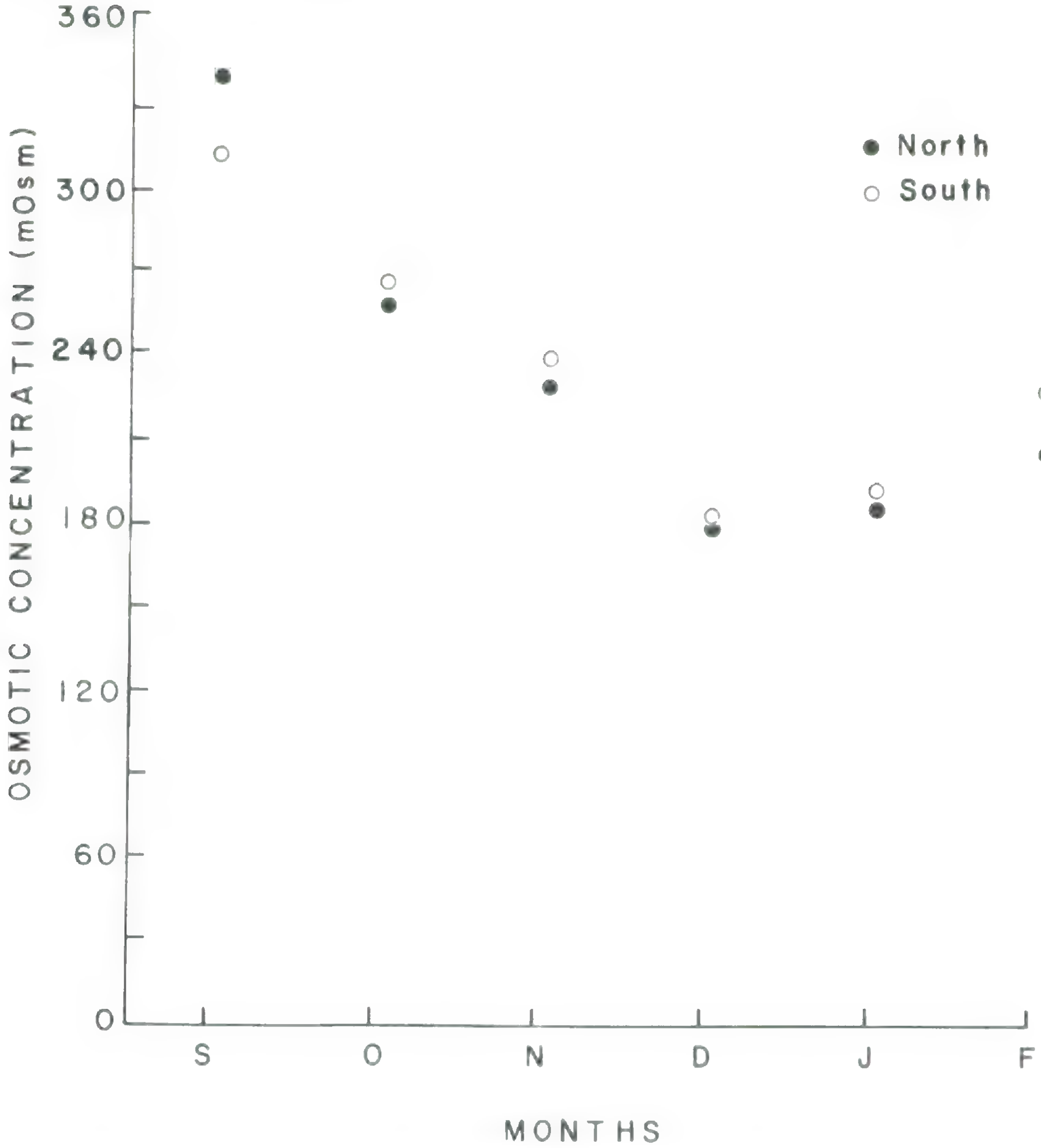

FIGURE 29.—Change in osmotic concentration (mOsm) of tissue fluids from sahuaro #202 at the Juniper site, Mohave County, Arizona, from September 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

parison of the depression of osmotic concentration from October to December (Fig. 30).

This coincided with the expected osmotic response due to available moisture through precipitation. It was also the reverse of what could be expected of a plant showing a tendency to show hardiness induced by response to cold.

With the dry period beginning in January and continuing through February, the concentration of plant tissue fluids again started to rise as the plant began to dry.

The low point of the curve (190 mOsm, January 1967; Fig. 30) has values quite close to the low point of other curves for this study (190.3 ±3.3 mOsm;

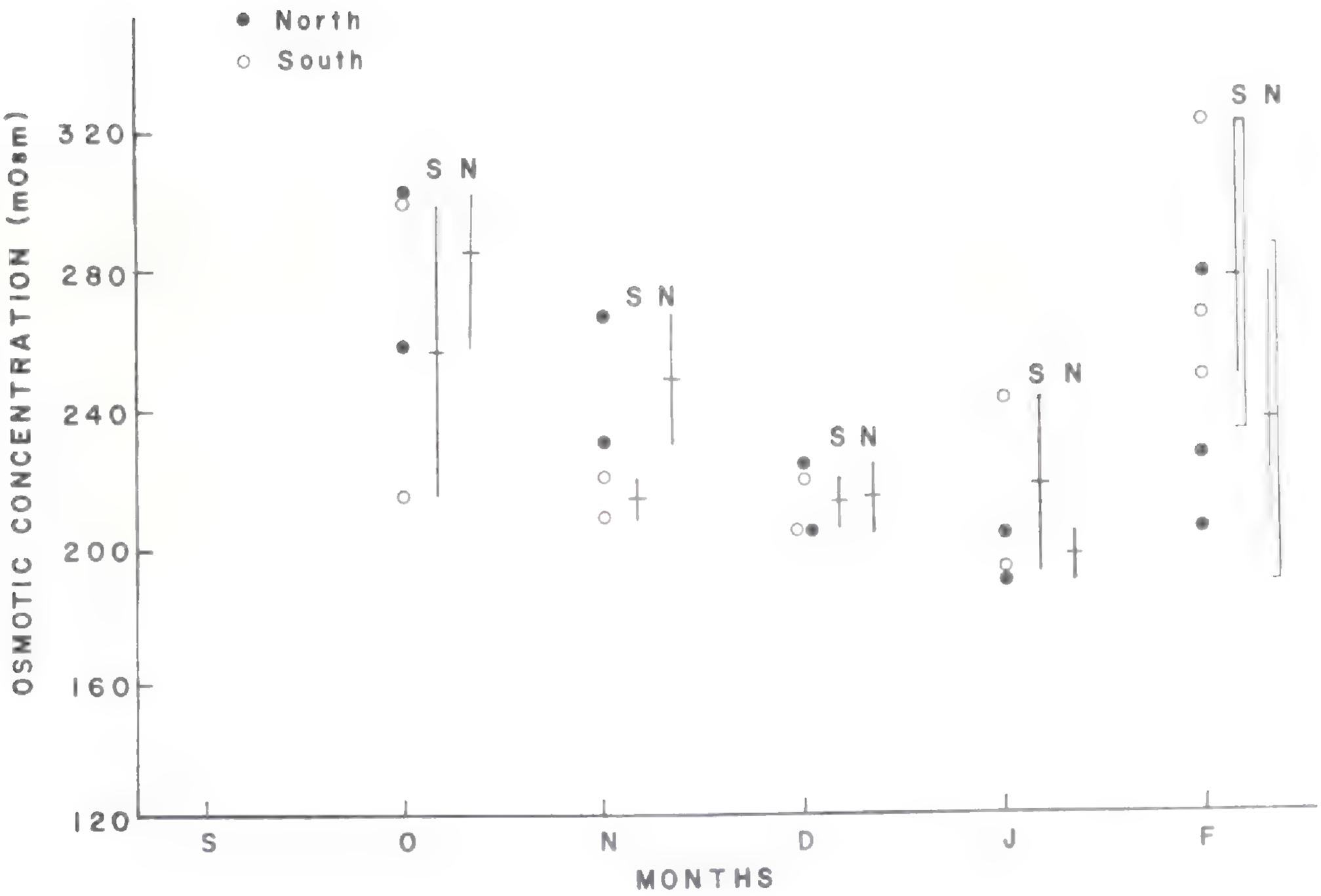

FIGURE 30.—Change in osmotic concentration (mOsm) of cortex tissue fluids from the sahuaro population at the Burro Creek monitoring site, Mohave County, Arizona, from October 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions are graphed for osmotic pressures on north and south sides of the sahuaros during February 1967.

Table 9). These values represent maximum observed hydration. Their similarity suggests a dilution point which is ordinarily not exceeded. The possibility that this is coincidental and represents a chance (random) point at which no more water was available to the plants is unlikely since it occurs repeatedly throughout the range of the sahuaro from southern Sonora to northern Arizona.

The comparison of the concentrations on the north and south sides of the plants was restricted due to small sample size. However, during the period of

TABLE 16. Order of sites on the Santa Catalina elevational transect. Ranking is from the highest to the lowest osmotic concentration of sahuaro cortex tissue fluids by site number and plant side (S, south; N, north.) September 1966–February 1967. 1 = 817 meter site, 2 = 869 meter site, 3 = 1067 meter site, 4 = 1170 meter site and 5 = 1317 meter site. The numbers in the table represent the sites, and the ordering is based on mean monthly osmotic pressure for each site as graphed in Fig. 45.

	Sept.		Oct.		Nov.		Dec.		Jan.		Feb.	
	S	N	S	N	S	N	S	N	S	N	S	N
highest	3	3	3	2	2	2	2	2	1	2	2	2
	2	2	4	4	3	3	1	4	3	3	1	3
	4	4	5	3	1	5	3	3	2	4	3	4
	1	1	2	5	4	4	4	1	4	1	4	1
lowest			1	1	5	1	5	5	5	5	5	5

hydration (October through December) the north was more concentrated; but when the rainy period ceased in January, the south sides again became more concentrated as the values on both sides rise (Fig. 30). This again suggests the greater sensitivity of the south side of the sahuaro to changes in levels of hydration.

South of Wikieup. The sahuaros south of Wikieup are on the south-facing slopes of low rolling hills (see Habitats). Four large plants were sampled a total of 14 times.

There was a significant ($P < .05$) decrease in the osmotic concentration of plant tissue fluids from the high initial reading (October 1966 = 266 mOsm)

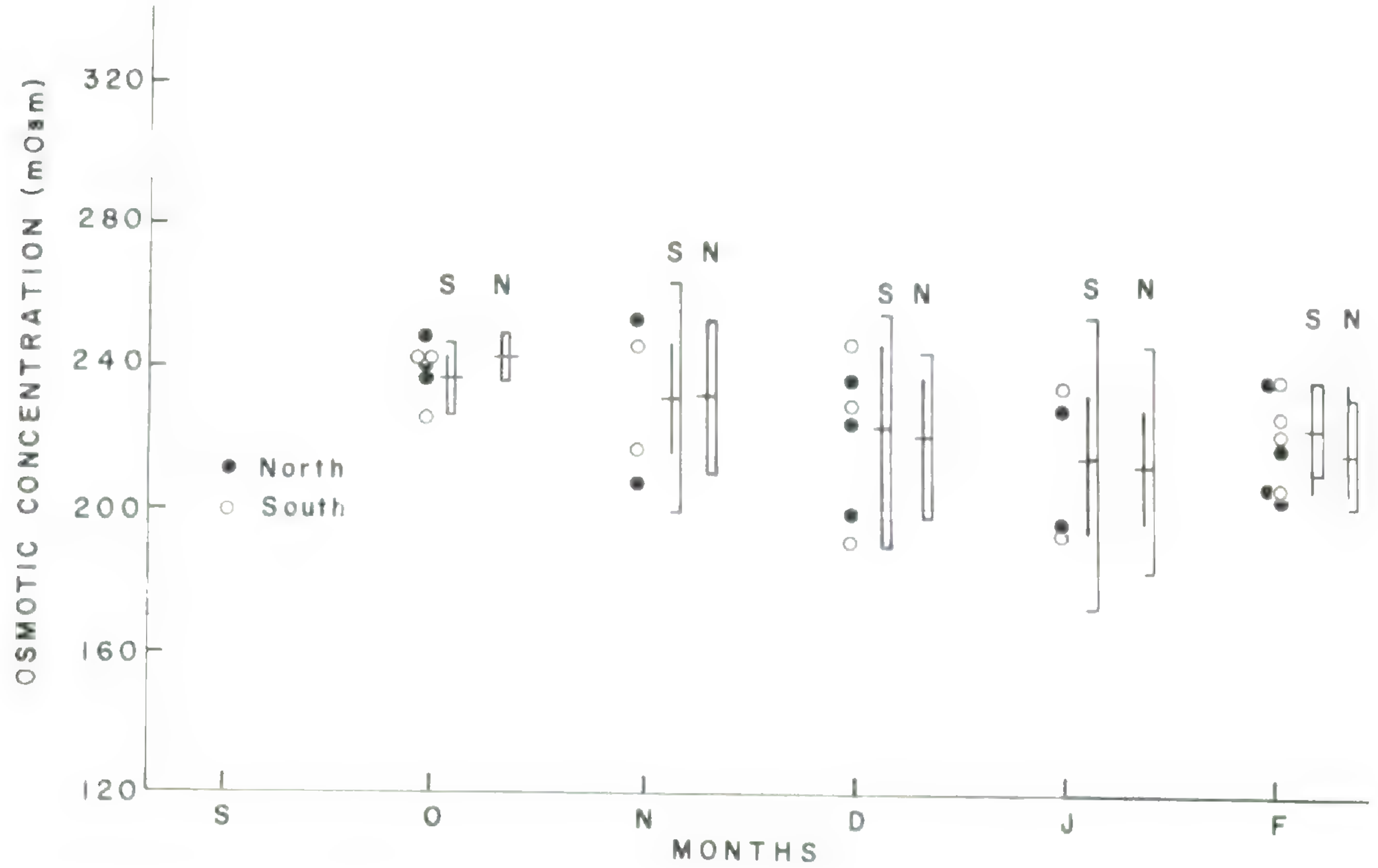

FIGURE 31.— Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids for the sahuaro population at the south of Wikieup site, Mohave County, Arizona, from October 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides. Frequency distributions calculated for osmotic concentrations on the south and north sides of the sahuaros at the south of Wikieup site.

to a low reading in January 1967 (191.4 mOsm; Fig. 31). Once again the steady decrease in osmotic pressure paralleled the pattern of increasing winter rainfall for late 1966 and early 1967.

The osmotic concentration curve for the population south of Wikieup (Fig. 31) followed those of the other stations at the northern end of the geographic distribution of the sahuaro, *i.e.*, north of the Santa Maria River. The lowest point on the curve (December = 189.5 mOsm) and the low mean values (January, north = 209.2 mOsm; January, south = 211.5 mOsm) are similar to the lowest values found along the physiological cline examined (Table 9).

South of Wikieup the difference between the means of the north and south sides of the plants throughout the five-month monitoring period is neither great (2–7 mOsm) nor significant.

North of Wikieup. This site is the farthest north in Arizona of those sampled for sahuaro cortex fluid concentration. Seventeen samples were taken from seven sahuaros. Here there was a significant reduction ($P < .05$) in osmotic pressure from the highest mean (240 mOsm) in September 1966 to the lowest mean (188 mOsm) in January 1967 (Fig. 32). This tempocline was broken by the cession of rains in January and February. At this time the plant tissue concentration started to rise again, the difference becoming significant after the 30-day period (Fig. 32).

The high initial values of the osmotic pressure (September and October, Table 11) at this site were significantly below those for the other northern sampling localities on comparable dates. This was not a result of the more northerly location having lower temperatures. Maximum-minimum thermometer records (Table 12) show that the site north of Wikieup had diurnal minima 5–7° C (9–13° F) higher and nocturnal minima 3–5° C (5–9° F) higher than the Juniper site in late 1966 and early 1967, as would be expected due to the lower elevation of the drier Wikieup site. Also temperatures from the recording weather station at Wikieup show September and October 1966 to be warmer than those for Tucson and almost as warm as those of Navojoa (see Climate and Weather). The lower end of the curve (November–February, Fig. 32) is similar to the values for comparable dates at the other sites monitored in the northern distribution of the sahuaro in east-central Mohave County and adjacent Yavapai County (Table 11).

Santa Catalina Elevational Transect

Santa Catalina Mountains (817 m). The change in concentration of sahuaro tissue fluids in this creosote bush association on the lower bajada of the Santa Catalina Mountains showed a significant ($P < .001$) increase through the first five months of the six-month monitoring period (Fig. 33). Four adult plants were sampled 14 times. One sample was taken from the north side only (plant #0-154, December 1966, Fig. 34).

The initial low values (September, 187–190 mOsm) increased to a maximum in January (320 mOsm). The effective rainfall during this period was minimal (Table 14).

TABLE 17. Extreme minimum and mean minimum monthly temperatures for the official recording weather station at Navojoa, Sonora, Mexico from January 1962 to June 1967.

Year and Month	Minimum Extreme ° C	Monthly Mean Minimum ° C	Year and Month	Minimum Extreme ° C	Monthly Mean Minimum ° C
1962			1965		
J	3.5	8.8	J	4.0	10.6
F	6.0	10.8	F	3.0	9.5
M	5.0	9.5	M	6.0	11.1
A	11.0	15.1	A	10.0	14.1
M	14.0	17.2	M	12.5	17.1
J	15.5	21.1	J	16.0	21.6
J	22.5	26.0	J	21.0	26.2
A	23.0	26.8	A	22.0	25.5
S	21.5	25.2	S	18.5	24.0
O	17.0	21.4	O	14.5	19.6
N	11.0	16.3	N	12.0	16.1
D	8.0	13.2	D	6.0	13.5
1963			1966		
J	1.5	9.4	J	5.5	9.5
F	7.0	11.3	F	5.5	9.1
M	8.0	11.7	M	6.0	11.6
A	10.0	13.6	A	14.0	16.6
M	14.5	19.2	M	15.0	20.8
J	17.0	23.1	J	21.0	24.7
J	22.0	26.3	J	23.5	26.4
A	22.0	25.1	A	23.0	25.0
S	21.0	25.0	S	20.0	24.5
O	18.0	21.1	O	15.0	18.8
N	11.0	14.9	N	8.0	14.5
D	7.0	12.4	D	3.0	10.7
1964			1967		
J	3.5	7.5	J	4.0	8.7
F	1.5	6.8	F	6.0	10.4
M	5.0	9.6	M	7.0	13.0
A	9.0	13.2	A	8.0	13.4
M	12.5	16.5	M	11.0	17.7
J	19.0	21.9	J	17.5	23.4
J	24.0	26.0			
A	22.0	25.1			
S	21.0	24.3			
O	17.0	21.7			
N	9.0	12.9			
D	8.0	11.2			

The pattern of osmotic concentration at this site, the initial rise broken by late winter rain, paralleled that of the other sample sites in the Tucson region. As elsewhere in the south (southern Arizona and southern Sonora) the high summer rainfall of 1966 was significant in producing the low initial values (Fig. 33). This high degree of hydration reduced directional differences to a minimum (September). The concentration of cortex tissue fluids increased following September due to a net water loss by the plants. As stated earlier the degree

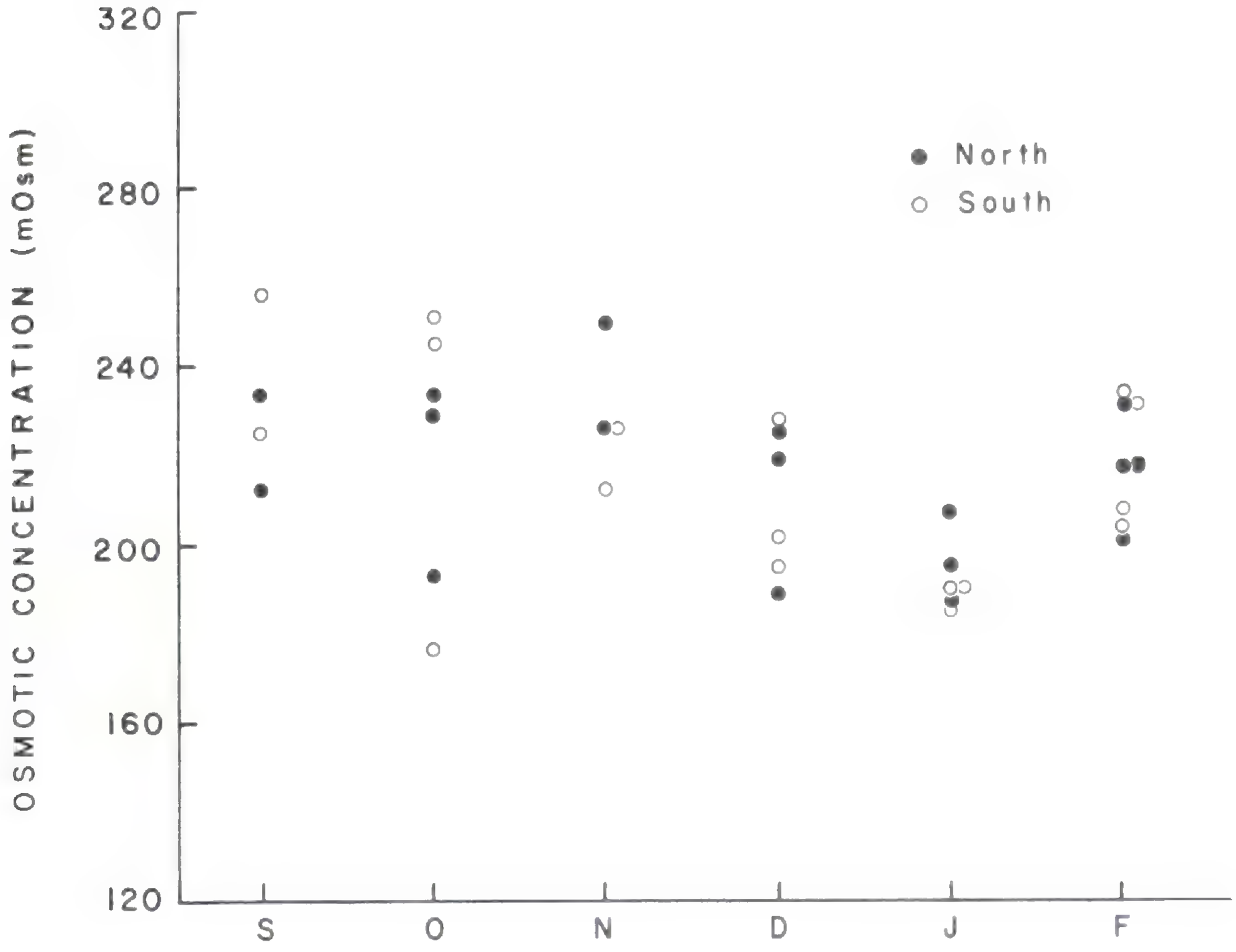

FIGURE 32.—Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids for the sahuaro population at the north of Wikieup site, Mohave County, Arizona, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

of this imbalance is influenced in part by tissue temperature, transpirational water loss, and precipitation. A combination of these factors produced water stress in the sahuaro, as evidenced by increasing osmotic pressures of the tissue fluid. The south sides of the sahuaros are more sensitive to changes of this type (Fig. 33), and from September through December the monthly increase in osmotic concentration of the cortex tissue was greater on the south side than on the north. While the sensitivity (change in osmotic pressure) to water loss is greater on the south side than the north, the sensitivity to water gain is also greater on the south side of the plant. The difference in response of the means of south to north from January to February was four-fold (south = 24 mOsm; north = 6 mOsm). This is to be expected of comparable tissues with different osmotic concentrations.

The single representative sahuaro (#0-154, Fig. 34) from this population showed a seasonal change in osmotic concentration. The values here are similar to those of the other Tucson locations discussed earlier. From a September low point at maximum observed hydration (186 mOsm), concentration of the sahuaro cortex fluid on the north side of this plant rose steadily throughout the six-month

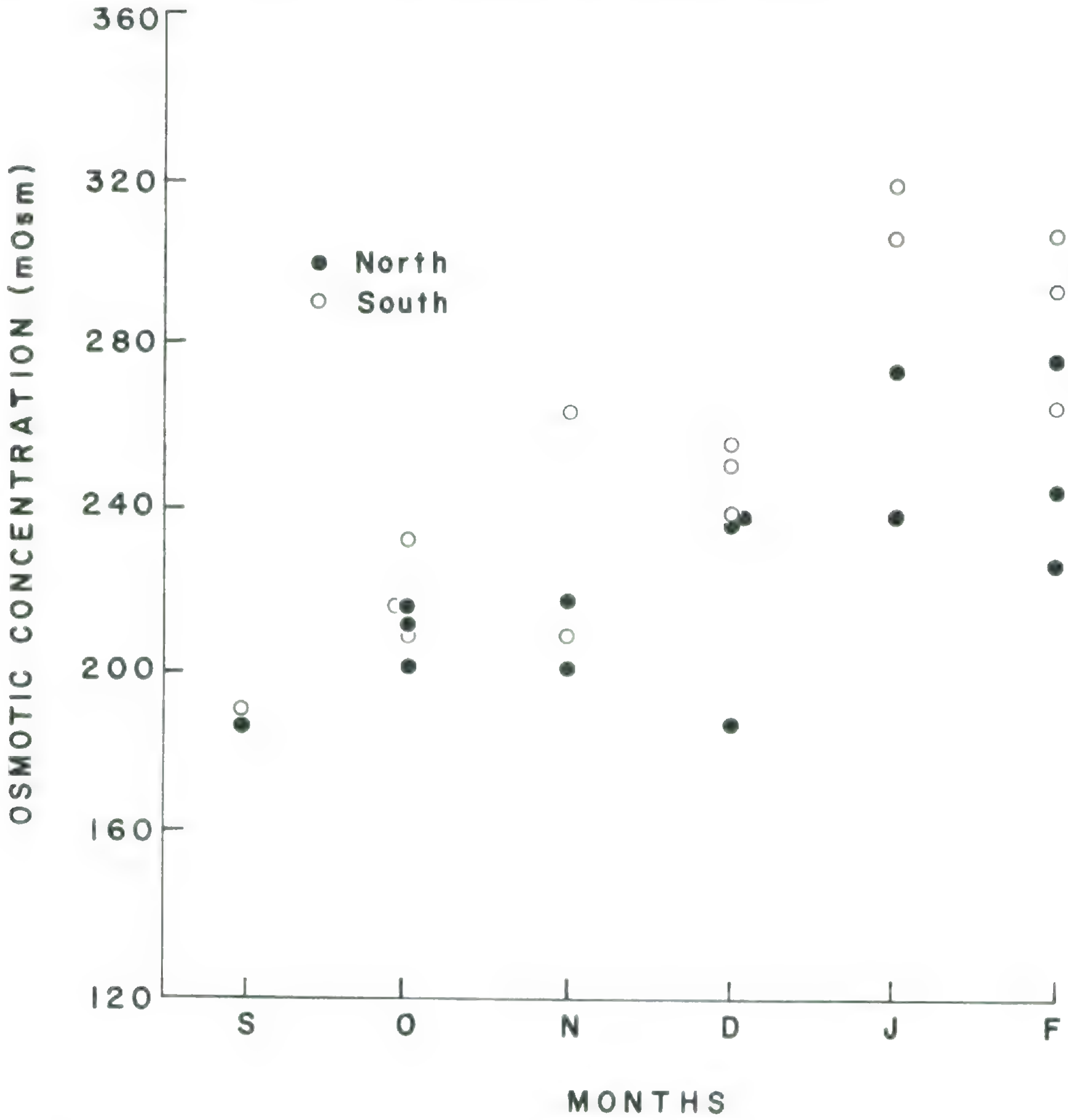

FIGURE 33.—Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids for the sahuaro population at the 817 meter site on the Santa Catalina elevational transect, Pima County, Arizona, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

monitoring period (Fig. 34). This reflects continued water loss in the face of transpirational demands. However, this loss is not as great as that on the south side of the plant which is normally exposed to higher tissue temperatures. The south side of plant #0-154 showed a greater sensitivity in February. While the concentration of the north side did not show a depression in February similar to that of the south (Fig. 34), the concentration of the north side on a population basis for February was reduced below the January mean (Fig. 33).

Santa Catalina Mountains (869 m). Four large sahuaros were sampled a total of 11 times at this site on the upper bajada of the Santa Catalina Mountains. The low initial readings in September and October are a result of the heavy summer rains (see Climate and Weather). A significant ($P < .001$) increase occurred

TABLE 18. Mean monthly temperatures for the 13 month period (June 1966–June 1967) bracketing the period of monitoring and the average mean monthly temperatures for Navojoa, Sonora, Mexico. Data for 1922–1962 from Hastings (1964), and Secretaria de Recursos Hidraulicos (1952).

Date	Monthly mean (1966–1967)	Monthly mean (1922 1962)
1966		
June	31.1° C	30.4° C
July	31.5	32.6
August	29.6	32.0
September	30.3	31.2
October	26.5	27.9
November	22.9	22.9
December	18.1	19.4
1967		
January	16.3	18.0
February	18.1	19.1
March	21.0	20.9
April	22.5	23.4
May	26.8	26.6
June	29.6	30.4

in the osmotic concentration through the six-month monitoring period (Fig. 35). In February a value of 358 mOsm, the highest recorded at any site during the monitoring period, and a total population mean of 320 mOsm (highest measured in the Santa Catalina area) reflected the lack of precipitation during the winter of 1966–67. This significant increase through a steady rise in osmotic pressure of sahuaro cortex fluids is similar to that of the other stations throughout the southern distribution of sahuaros during this period.

The edaphic conditions here suggest greater available soil moisture at this site than on the lower bajada, 817 m. The higher percentages of large soil particle size (Table 13, Fig. 36) in this paloverde-sahuaro (*Cercidium-Cereus*) community provide greater available soil moisture (Yang & Lowe, 1956), but this is not reflected in a comparison of the osmotic pressures of the sahuaros on these two sites. Also the bajada locality is located at the base of the Santa Catalina temperature inversion (Shreve, 1912, 1914, 1922). The resulting lower nocturnal and minimum temperatures reduce the overall heat load on the sahuaros. This reduction did not lower the net loss of water by the plants as would be expected (Kramer & Kozlowski, 1960).

Santa Catalina Countains (1067 m). The seasonal trend at this site was similar to that at other sites on this elevational transect. The increase in the concentration of plant tissue fluids from the lowest values in October to the highest in January was significant ($P < .001$, Fig. 37). Thirteen samples were taken from five plants.

The reduction in evapo-transpiration with increase in elevation contributed to the reduced rate of increase in concentration. Being located at the upper end of the Santa Catalina temperature inversion, these sahuaros potentially lose more water during the night than might otherwise be expected of plants at this elevation,

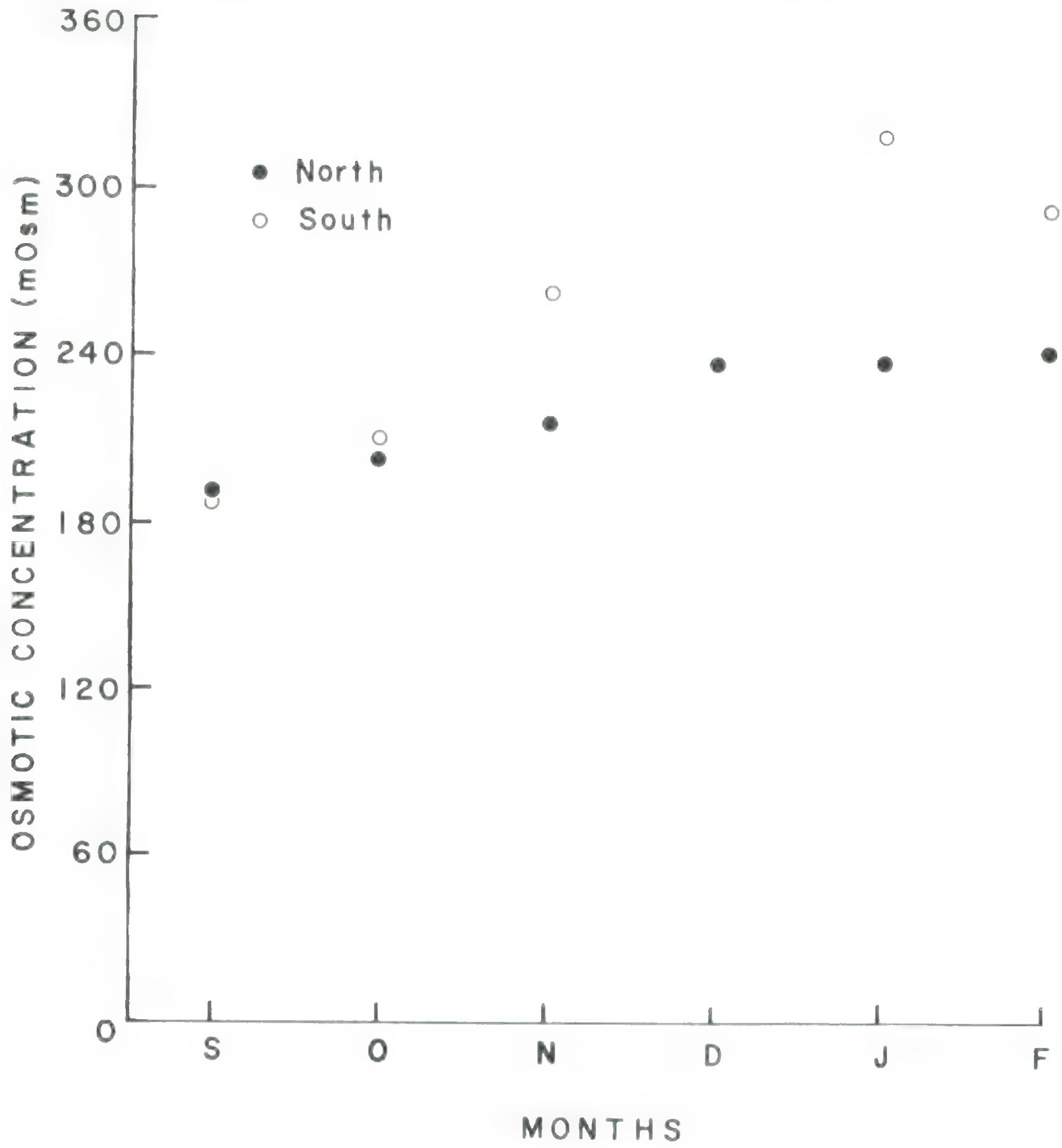

FIGURE 34.—Change in the osmotic concentration of sahuaro #0-154 at the 817 meter site on the Santa Catalina elevational transect from September 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

due to the higher nocturnal temperatures. However, these higher temperatures also reduce the danger of cold damage. The higher elevation at this site (200 m above the next lower site) intensifies the effect of single rains and causes a greater change in the freezing point depression of the tissue fluids (Fig. 37).

Santa Catalina Mountains (1170 m). At a point of wide-spread directional freeze damage in the Santa Catalina Mountains, one can assume that the surviving plants are relatively cold-resistant. Almost every sahuaro over two meters in height has scar tissue on the southeast side dating back to the freeze of January 1962. The new growth above the scarring shows the small amount of permanent damage to this population. Seventeen samples were taken from eight sahuaros.

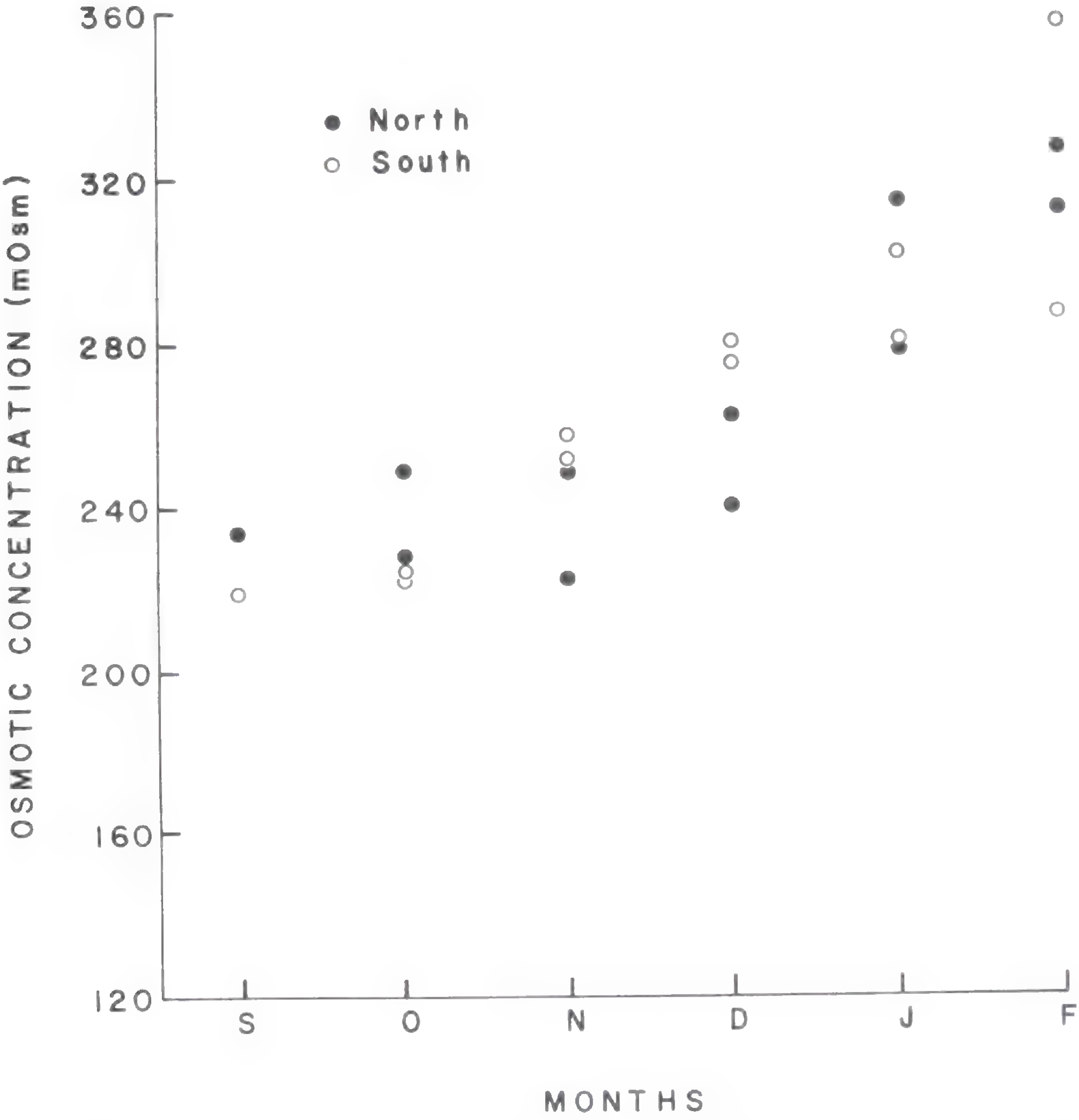

FIGURE 35.—Change in osmotic concentration of sahuaro cortex tissue fluids of the sahuaro population at the 869 meter site on the Santa Catalina elevational transect, Pima County, Arizona, from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

The response of the plant tissue fluid concentration to the lack of precipitation is evident in the significant ($P < .001$) increase in the values from September to February (Fig. 38). The initial readings were lower than comparable readings at sites at lower elevations; this continued throughout the monitoring period with the final and highest concentrations (February) being lower than the three sites below 1170 m on the transect (1067, 869, and 817 m). Even though the values for the population started lower (*ca.* 200 mOsm), ended lower (*ca.* 270 mOsm), and had a smaller amplitude than the other three sites, the same increase in osmotic concentration with lack of precipitation appeared here as it did elsewhere in southern Arizona and southern Sonora.

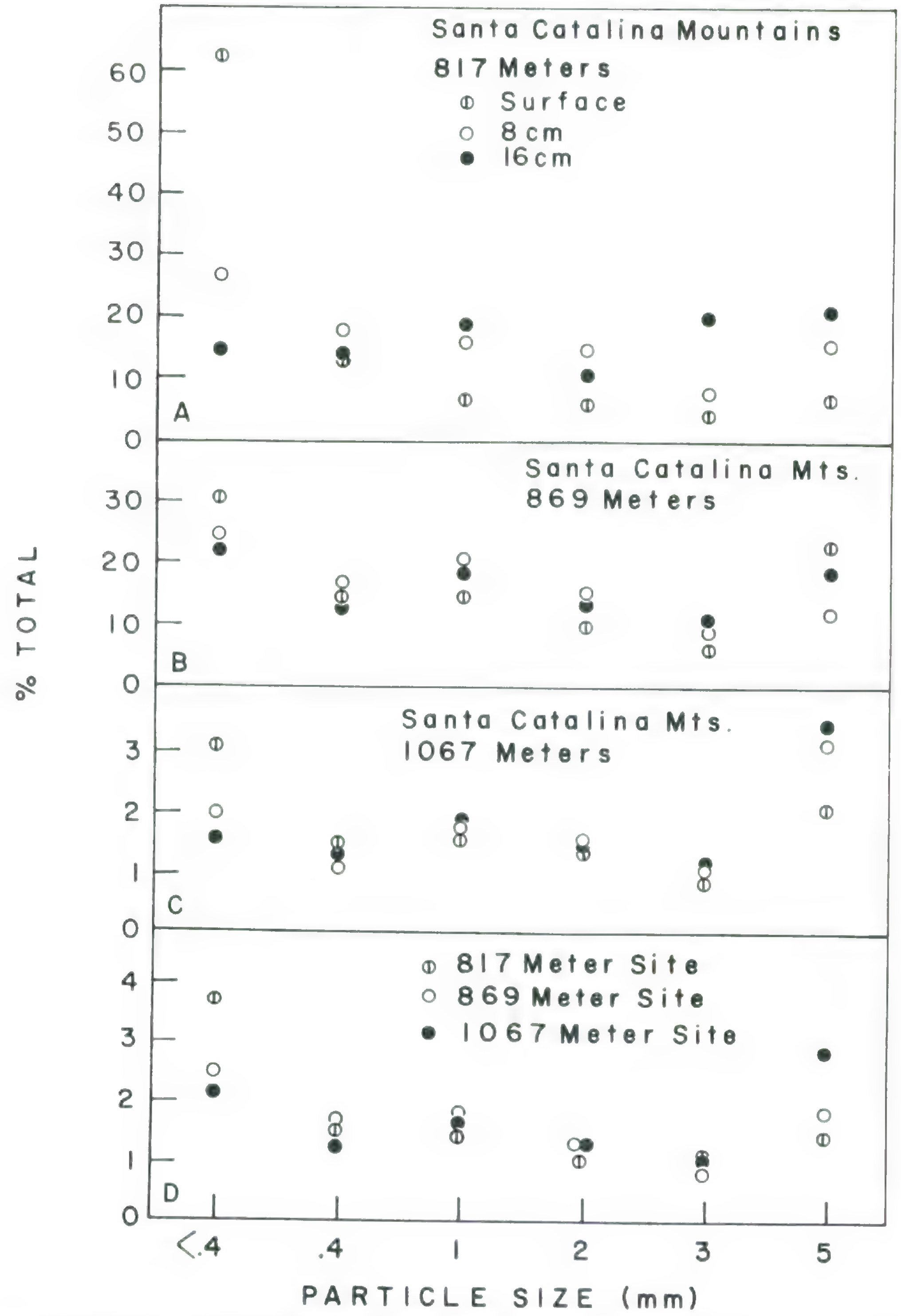

FIGURE 36.—Physical properties of soils representative of the monitoring sites on the Santa Catalina elevational transect. Soils collected from depths of 4 cm (open circles), 15 cm (closed circles), and from the surface (hatched circle) at the 817 meter site (A), 869 meter site (B) and 1067 meter site (C). Mean values of the three depths at each site are graphed (D).

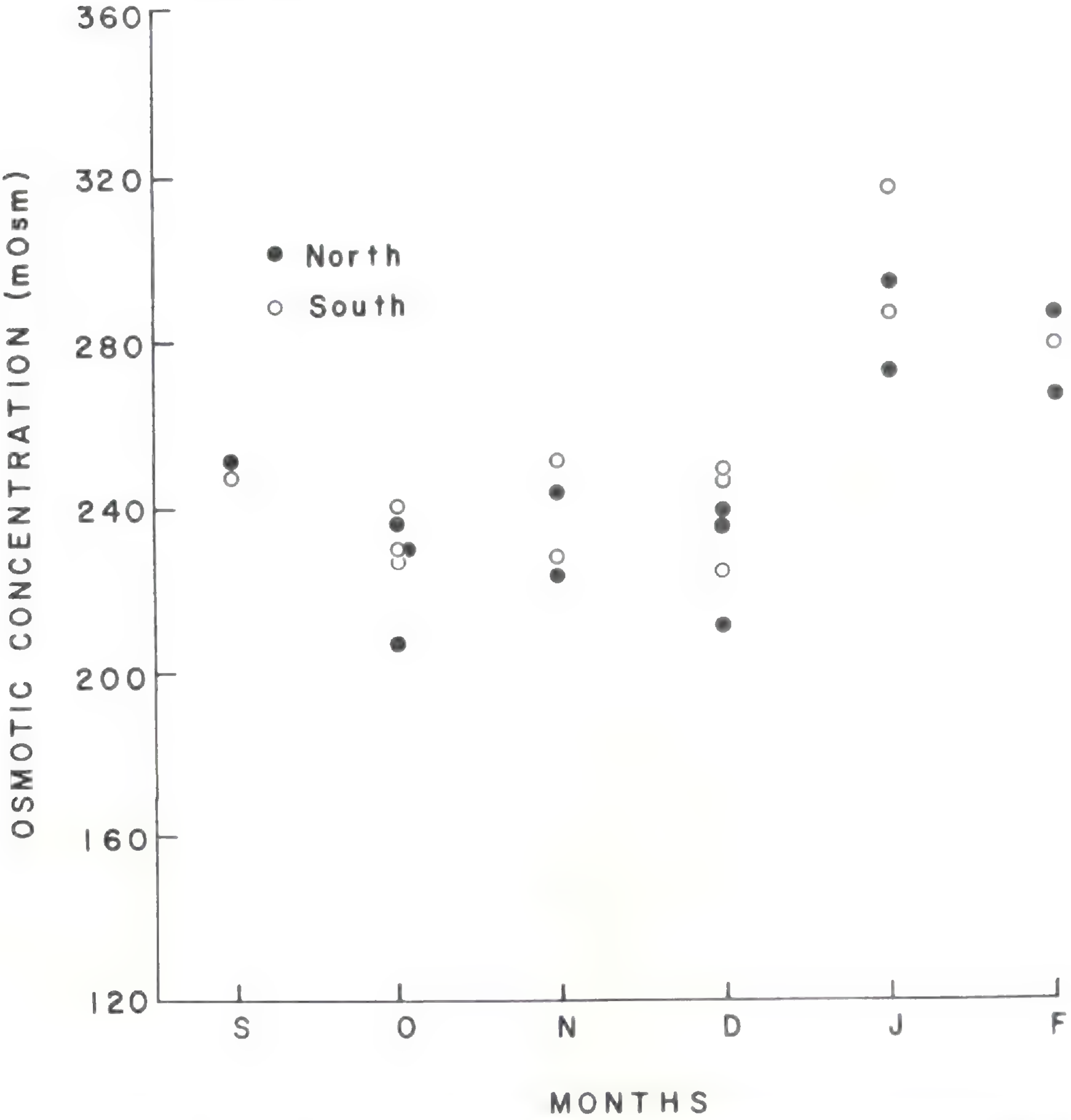

FIGURE 37. Change in osmotic concentration of sahuaro fluids of the sahuaro population at the 1067 meter site on the Santa Catalina elevational transect September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

The increased elevation with corresponding decreased stress due to moisture factors reduced water demands of and on the sahuaros. This accounted for the low initial readings and the relatively small rise during the monitoring period.

A single plant (#0-152) is representative of the reduced freezing point depression of tissue fluids on a population basis at this site (Fig. 39). It also reflected the reduction in the difference between the concentration of plant tissue fluids on the north and south sides of the plant. This was to be expected in plants having reduced water demands after they had been recently hydrated. The higher elevation and the associated moisture factors (see Lowe, 1967*a*) did not place as heavy a demand on the south side as did the microenvironmental conditions at lower elevations.

The increased precipitation at this elevation and reduced evapo-transpiration

TABLE 19. Mean monthly temperatures from June 1966–June 1967 and the average mean monthly temperatures (1940–1966) for Tuscon International Airport, Pima County, Arizona. Data from Department of Commerce (1966*b*, 1967*b*).

Date	Monthly mean temperature from June 1966–June 1967	Average monthly mean
1966		
June	28.2° C (82.8° F)	28.2° C (82.7° F)
July	29.6° C (85.3° F)	30.2° C (86.3° F)
August	28.3° C (82.9° F)	28.4° C (83.1° F)
September	25.7° C (78.3° F)	26.9° C (80.4° F)
October	20.5° C (68.1° F)	21.1° C (70.0° F)
November	16.2° C (61.1° F)	14.5° C (58.1° F)
December	11.3° C (52.4° F)	11.1° C (51.9° F)
1967		
January	10.8° C (51.4° F)	9.9° C (49.8° F)
February	13.2° C (55.6° F)	11.6° C (42.9° F)
March	16.7° C (62.1° F)	14.5° C (58.0° F)
April	16.7° C (62.1° F)	18.8° C (65.9° F)
May	22.2° C (71.9° F)	23.1° C (73.5° F)
June	27.1° C (80.7° F)	28.2° C (82.7° F)

decreased the water stress on the sahuaros at this site. The increase in concentration of the plant tissue fluids during the study at this site shows that this stress was only reduced, not eliminated.

Santa Catalina Mountains (1317 m). Although sahuaros are found higher in the Santa Catalinas (over 1525 m), this population represents the highest stand readily accessible on the Mt. Lemmon Highway transect. Ten samples were taken from three plants. Two of the three, along with many others, were killed during a range fire during the summer of 1967.

The characteristic curve of plants under a condition of net water loss was found in this uppermost population (Fig. 40). Initial values here (October mean 220 mOsm) are slightly lower than comparable values for the site immediately below (Santa Catalina Mountains, 1170 m; October mean 230 mOsm). The increase for the population is not as sharp as other points on this elevation but is still significant ($P < .001$). The final and highest concentrations (February, *ca.* 260 mOsm) are significantly higher than the October values but less than those of comparable readings for other stations on the transect. These factors suggest that the water stress at this point is less than that at the other points along the Santa Catalina elevational transect, yet the stress still exists as shown by the significant increase in the osmotic concentration of the cortex fluids.

DISCUSSION

Osmotic Concentration. In southern Sonora the osmotic concentration of sahuaro cortex fluids was lowest at the beginning of the monitoring period (September 1966). This followed the second wettest August on record; also the period prior to monitoring had more rain than the total for the full six-month monitoring period at the other sites (Table 14).

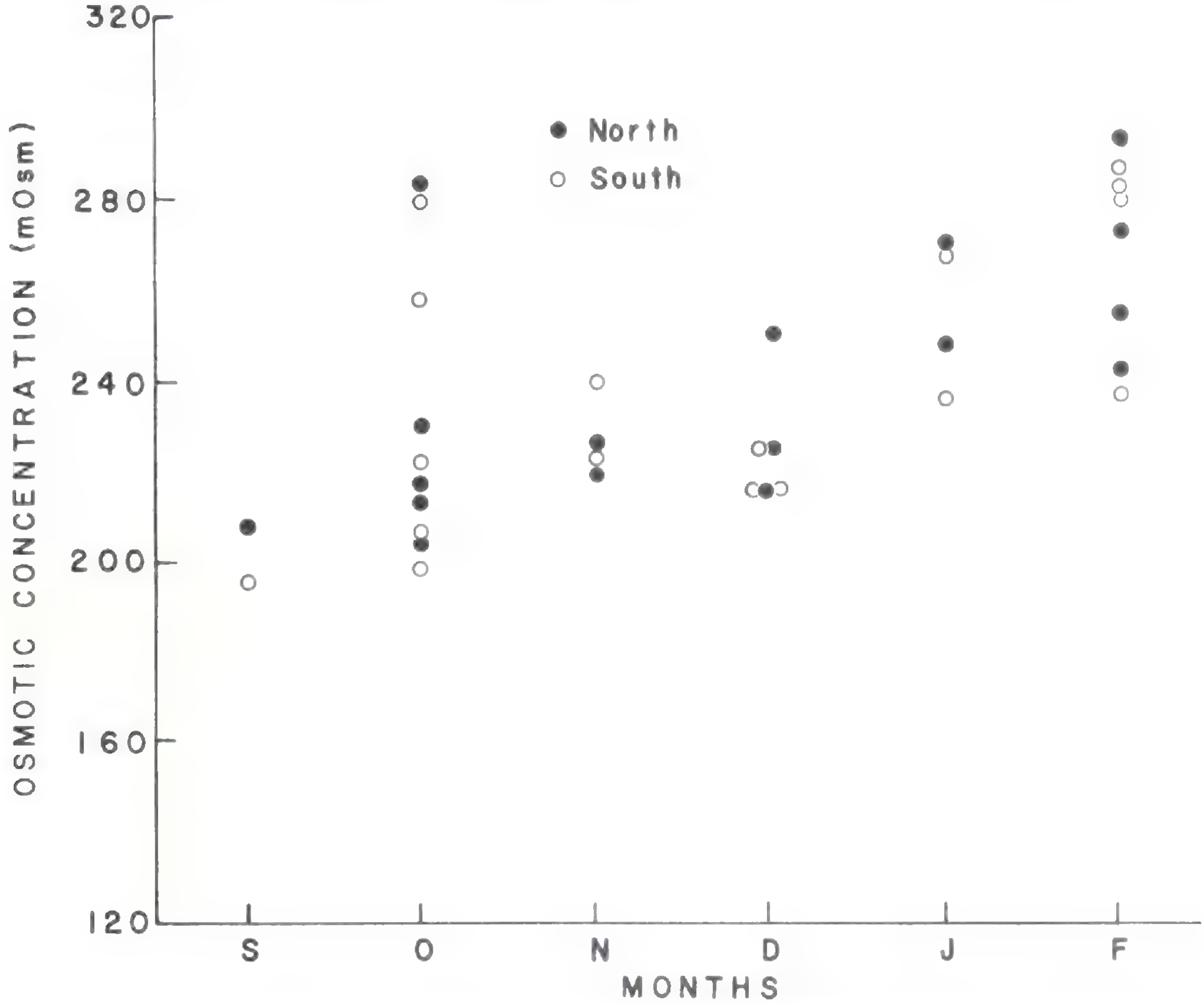

FIGURE 38.—Change in osmotic concentration of sahuaro cortex fluids of the sahuaro population at 1170 meters on Santa Catalina elevational transect from September 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

There was a significant increase in concentration of sahuaro cortex fluid during the monitoring period based on change in concentration of the south and north sides of the plants ($P < .05$, Fig. 41). This increase was significant from September and October to February. In addition the increases from October to November and November to December on the south sides were also significant ($P < .05$). These two periods had no measurable precipitation (Table 14). The mean and extreme values were higher for January and February, but this increase was not significant ($P > .05$) and there was precipitation during these months (Table 14). The lack of "effective" rainfall prior to the February sampling coupled with no significant increase in concentration could be due to greater on-site precipitation or a carryover of the effect of the rainfall prior to the January sampling.

In months showing significant increases in concentration (November and December) there was also a significant difference ($P < .05$), with the concentration of the south side higher than that of the north side of the plants for each month (Fig. 41). The significant difference between south and north continued through February (Table 15), but the monthly significant increase was not maintained. This coincided with the resumption of precipitation at the end of

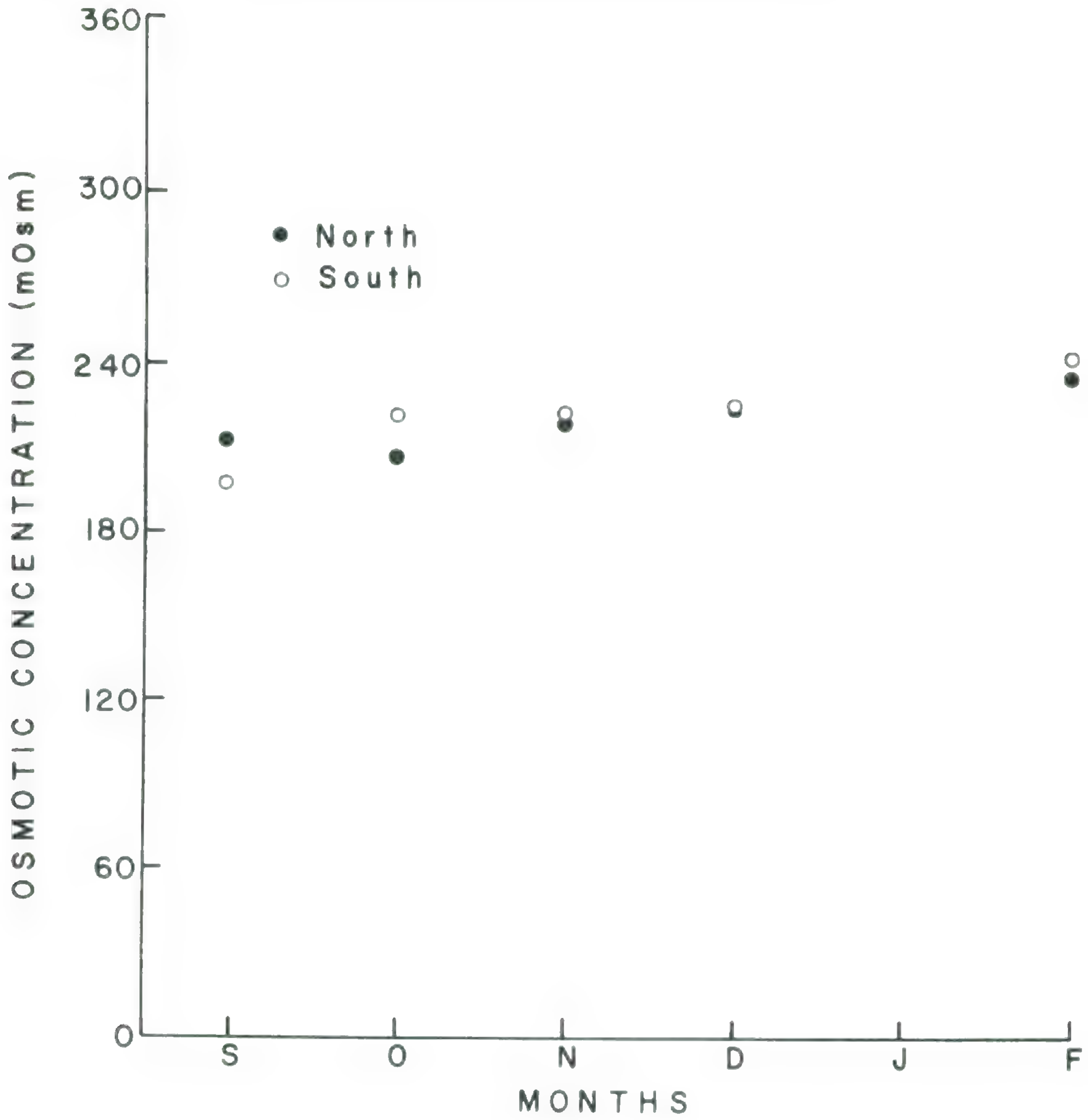

FIGURE 39.—Change in osmotic concentration of sahuaro #0-152 at the 1170 meter site on the Santa Catalina elevational transect from September 1966 to February 1967. Open circles, south side of sahuaro; closed circles, north side.

December. There was a continual increase from month to month on both the south and north sides. However, the change was never significant on the north side on a month to month basis, and it was only significant on comparison at two month intervals. The concentration on the south sides also rose each month. Here the rise was only significant in months with no effective rainfall and the January sampling period which had only one heavy rainfall late in December.

In the Tucson region of southern Arizona there was a significant increase ($P < .05$) in the osmotic concentration of plant tissue fluids from early low values (September and October) to final high values (January and February) as determined from change in concentration of both the south and north sides of the sahuaros (Fig. 42). Initially the concentration was diluted by the precipitation prior to the September and October monitoring (Table 14). While there

was little rainfall between the October and November readings, November values were not higher. This was due in part to a carryover effect of hydration from earlier months. The rise in December on north and south was not significant ($P > .05$), but by January this was significant ($P < .05$, Fig. 42). The rise did not continue into February but levelled off as it did in Sonora.

A comparison of the values for southern Sonora and the Tucson region shows them to be not significantly different in September and October, but the readings for Tucson are significantly lower in November and December (Fig. 43). The lack of any measurable precipitation in southern Sonora accounted for the rise in concentration during November and December. The measurable but "ineffective" rainfall at Tucson during these months and the associated change in osmotic concentration suggests greater on-site precipitation. The January values were not significantly different and both areas had rainfall over 0.2 inches during the period.

Throughout the monitoring period the concentration was higher on the south than on the north sides (Fig. 42). This was significantly higher only during the monitoring periods of October, December, January, and February ($P < .05$). The general increase in concentration in January was accompanied by significant increases in both the north and south tissues over the values for the previous month.

In northern Arizona there was a steady decrease in osmotic concentration during the monitoring period from the high initial readings in September 1966 to the low values in January 1967 (Fig. 44). On a month to month basis the decrease was not significant ($P > .05$) on either side of the plants, but on comparison of the high initial values in September and October with the low readings in December and January, the decrease is significant ($P < .05$) on both sides of the plants (Fig. 44). In each of the first four months of the monitoring period there was effective precipitation coming in heavy falls (1.10 inches (27.9 mm) on Sept. 19; 0.77 inches (19.6 mm) on Oct. 4–5; 1.02 inches (25.9 mm) on Nov. 9; and 1.80 inches (45.7 mm) on Dec. 4–7). Even though only 0.1 inch of precipitation fell prior to the January monitoring, the sahuaros were still responding to the heavy rain of fall and early winter. The February monitoring period showed significant osmotic increase ($P < .05$) over January (Fig. 44) on both south and north sides. This coincided with the decrease in precipitation in January and February.

Throughout the period of hydration (period of decreasing osmotic concentration, September–January) the south side was never significantly ($P > .05$) higher than the north. As with the general concentration, the south and north decreased significantly during the period of hydration (September to January) and increased significantly ($P < .05$) in February above the previous values for the two sides in January.

In summary, in southern Sonora there was a monthly increase in the concentration of sahuaro fluids during the six-month monitoring period, September 1966–February 1967. During the months with rainfall there was no significant increase in concentration, while there was a significant increase during months with no measurable precipitation.

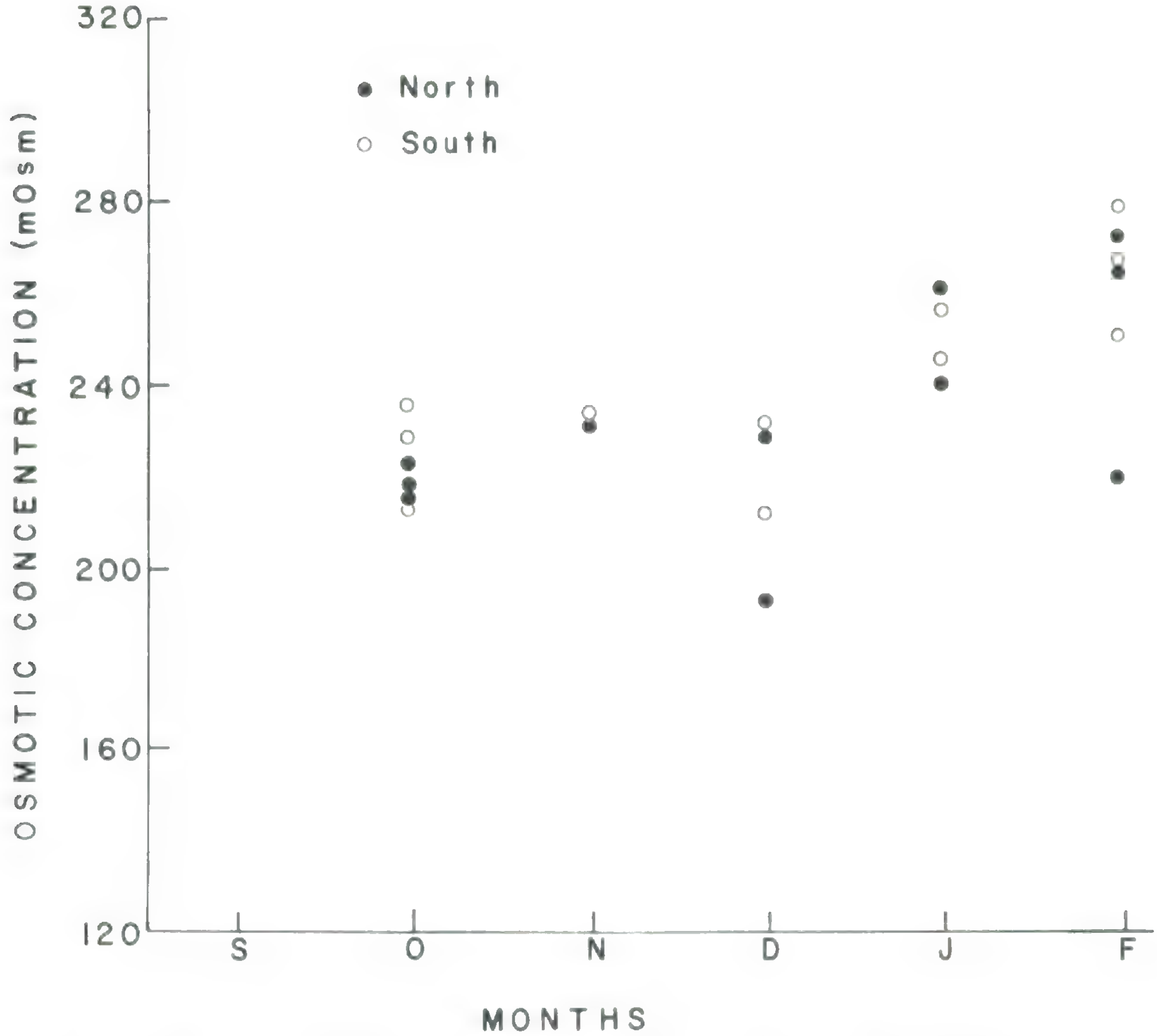

FIGURE 40.—Change in osmotic concentration (mOsm) of sahuaro cortex fluids of the sahuaro population at the 1317 meter site on the Santa Catalina elevational transect, Pima County, Arizona, from October 1966 to February 1967. Open circles, south sides of sahuaros; closed circles, north sides.

The difference between south and north sides during the same month was also significantly higher on the south during months with no measurable precipitation as well as January. Each month showed an increase in the concentration of the south sides and the north sides. On the north this was never significant on a monthly basis, but it was significant in comparison of two month intervals. On the south the increase was significant on a month to month basis during periods of no rainfall.

In the Tucson region there was a significant increase in concentration. The low initial values here, as in southern Sonora, were influenced by the heavy late season rains. With the stoppage of the rains the concentration of the plant fluids started to rise in December. The increase became significant in January. The February reading leveled off here as in southern Sonora.

The concentration on the south was higher than on the north side each month. This was significant in October, December, January, and February ($P < .05$). The increase from month to month for each side was only significant once (Jan-

TABLE 20. Mean monthly minimum and extreme minimum temperatures for the 13 month period (June 1966 June 1967) bracketing the period of monitoring and the average mean monthly minimum based on temperature from the recording station at the Tucson International Airport from 1940–1966.

Date	Monthly mean minimum temperature, June 1966 June 1967	Extreme monthly minimum temperature, June 1966 June 1967	Monthly mean minimum temperature, 1940 1966	Record monthly minimum temperature and year
1966				
June	19.8 C (67.6 F)	13.3 C (56 F)	19.5 C (67.1 F)	+8.3° C (47° F), 1955
July	22.7 C (72.8 F)	18.9 C (66 F)	23.4 C (74.1 F)	17.2° C (63 F), 1960
August	22.1 C (71.7 F)	20.0 C (68 F)	22.0 C (71.5 F)	16.1 C (61 F), 1956
September	19.4 C (66.9 F)	17.2 C (63 F)	19.7° C (67.4 F)	+6.7 C (44° F), 1965
October	11.7 C (53.1 F)	-6.1 C (43 F)	13.8 C (56.8 F)	+1.7 C (35 F), 1949
November	+8.1 C (46.7 F)	0.0 C (32 F)	+6.8 C (44.2 F)	4.4° C (24 F), 1958
December	+3.8 C (38.8 F)	5.0° C (23° F)	+3.8 C (38.9 F)	7.8 C (18 F), 1954
1967				
January	+1.9 C (35.5 F)	6.7° C (20° F)	+2.8° C (37.0° F)	8.9° C (16° F), 1949
February	+4.3 C (39.8 F)	1.1 C (30° F)	+4.3 C (39.8° F)	6.7° C (20° F), 1955[a]
March	+8.1 C (46.5 F)	0.0° C (32° F)	+6.6° C (43.8° F)	6.7° C (20° F), 1965
April	+8.2° C (46.7 F)	+1.1° C (34° F)	10.3 C (50.6° F)	-2.8° C (27° F), 1945
May	13.4° C (56.1 F)	-3.9° C (39° F)	14.2 C (57.5° F)	+3.3° C (38° F), 1950
June	19.0° C (66.2 F)	12.8 C (55° F)	19.5 C (67.1° F)	+8.3° C (47° F), 1955

[a] Record equalled in earlier years

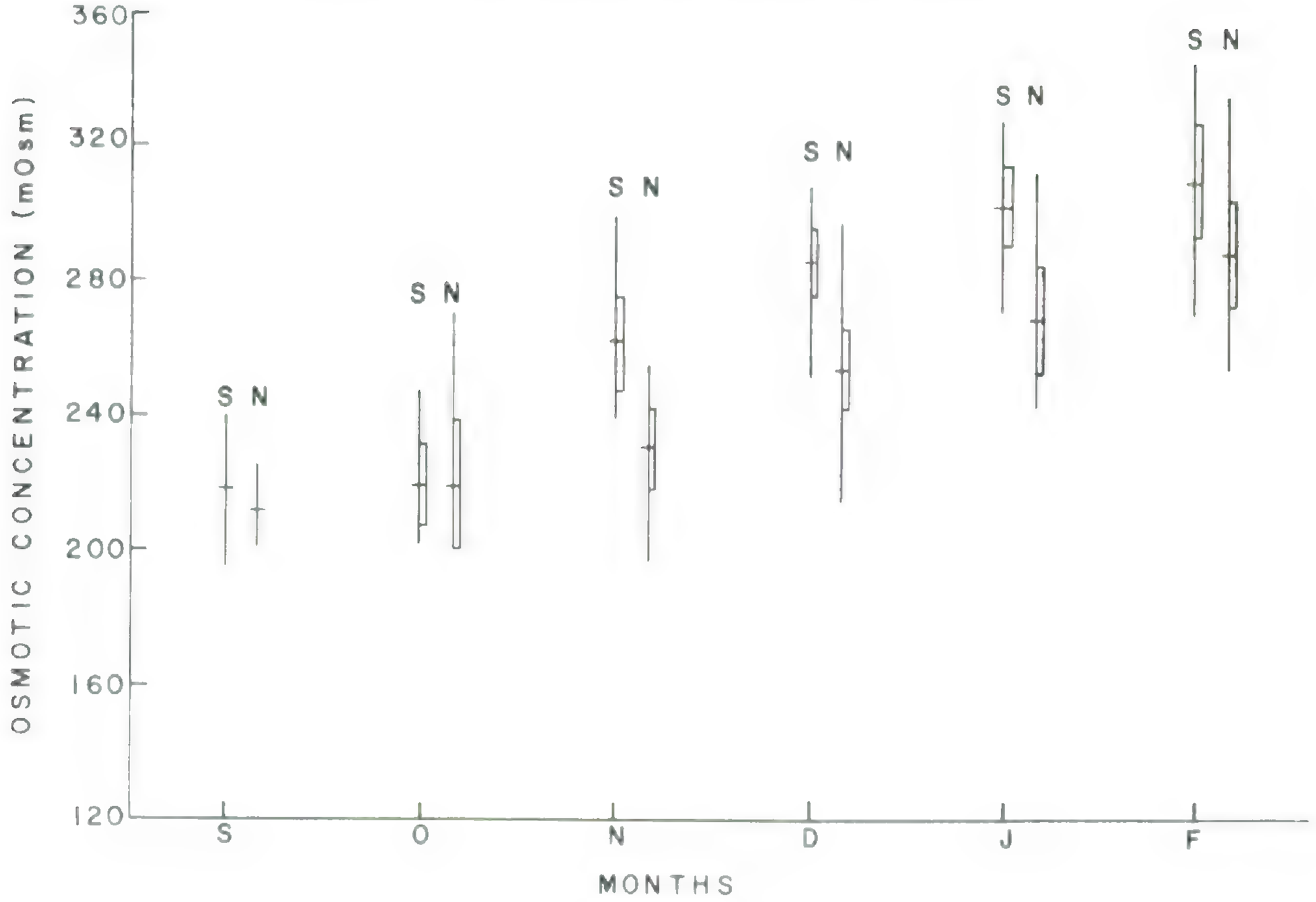

FIGURE 41.—Southern Sonora. Change in osmotic concentration of cortex tissue fluids for sahuaro populations at the sampling sites in southern Sonora, Mexico, from September 1966 to February 1967. Frequency distributions graphed for the osmotic concentrations on the south (S) and north (N) sides of the sahuaros.

uary). The final readings for the south and north for January and February were significantly higher than those for the early part of the monitoring period.

A comparison of osmotic concentrations for southern Sonora versus Tucson, Arizona, showed no significant difference during the initial monitoring periods of September and October 1966. The values in Tucson were significantly lower in November and December, suggesting greater on-site precipitation on the bajadas; prior to these two readings no precipitation was recorded in southern Sonora. In January—a month showing effective rainfall in both places, but more in Sonora—there was no significant difference.

In northern Arizona there was a steady decrease in osmotic concentration paralleling high rainfall. The decrease became significant in December in respect to the September and October readings. A significant increase in concentration in February followed a period of little effective rain in January and February.

There was no significant ($P > .05$) difference between south and north sides of the sahuaros in any single month of the monitoring period from September to January with the exception of November when the north was higher ($P < .01$). However, there was a significant decrease of both sides during the period of hydration (September to January) and significant increase of both in February.

Differential Concentration—Southern Arizona. In the Tucson area (bajadas of the Tucson Mountains and the Santa Catalina Mountains), the pattern was similar to that in southern Sonora. In September the concentration of the sahuaro

TABLE 21. Extreme high temperatures and monthly mean maximum temperatures for the monitoring period at representative stations along the latitudinal transect through the geographic range of the sahuaro (June 1966 February 1967).

Site	Extreme maximum and date	Mean monthly maximum and date
Navojoa, Sonora, Mexico	41.5° C, 23 Sept. 1966	37.5° C, July 1966
Tucson International Airport	40.5° C, 25 June and 6 July 1966	36.8° C, June 1966
University of Arizona, Tucson	42.8° C, 25 and 26 June 1966	39.6° C, July 1966
Tucson Magnetic Observatory	41.1° C, 16 and 26 June 1966	37.8° C, July 1966
Wikieup, Arizona	43.9° C, 5 August 1966	40.2° C, July 1966

cortex fluid was not significantly higher on the south sides than on the north ($P > .05$; Table 15, Figs. 21, 24, 33). However, it was significant ($P < .001$) from October through February. This similar response between southern Sonora and southern Arizona was also matched by the similar rainfall patterns immediately before and during the period of monitoring. Both areas had summers wetter than normal and extremely heavy late summer precipitation (see Climate and Weather).

Differential Concentration—Northern Arizona. The northern end of the geographical distribution of the sahuaro from the Santa Maria River to north of Wikieup had a different precipitational pattern prior to and during the six-month monitoring period than was found to the south. Here the summer was unusually dry and the late summer-early winter months (September–December) were wetter than normal (see Climate and Weather). During the period of greater precipitation the south side was not significantly higher ($P > .05$) than the north side of the plant (Table 15; Figs. 26, 28, 30–32). And in November the concentration on the north was even higher than the south ($P < .01$, Table 15). This rise of the concentration on the north in November can not be explained on the basis of precipitation alone. The rainfall for this month was above average. This was an increase over the previous month, October, and less than the following month, December (see Climate and Weather). Also the higher concentration on the north side did not persist into December. However, November is the first month in this region in which the sahuaros were subjected to freezing temperatures. With a mean monthly minimum of +5° C, in November 1966 the sahuaros were placed under the first severe low thermal stress of the winter. It is possible that the significantly higher concentration on the north side represented a hardiness factor that eventually was washed out or diluted by the heavy December rains. The first freezing temperatures of the winter also occurred in Tucson in November. However, the south sides were higher at these sites due to the lack of precipitation.

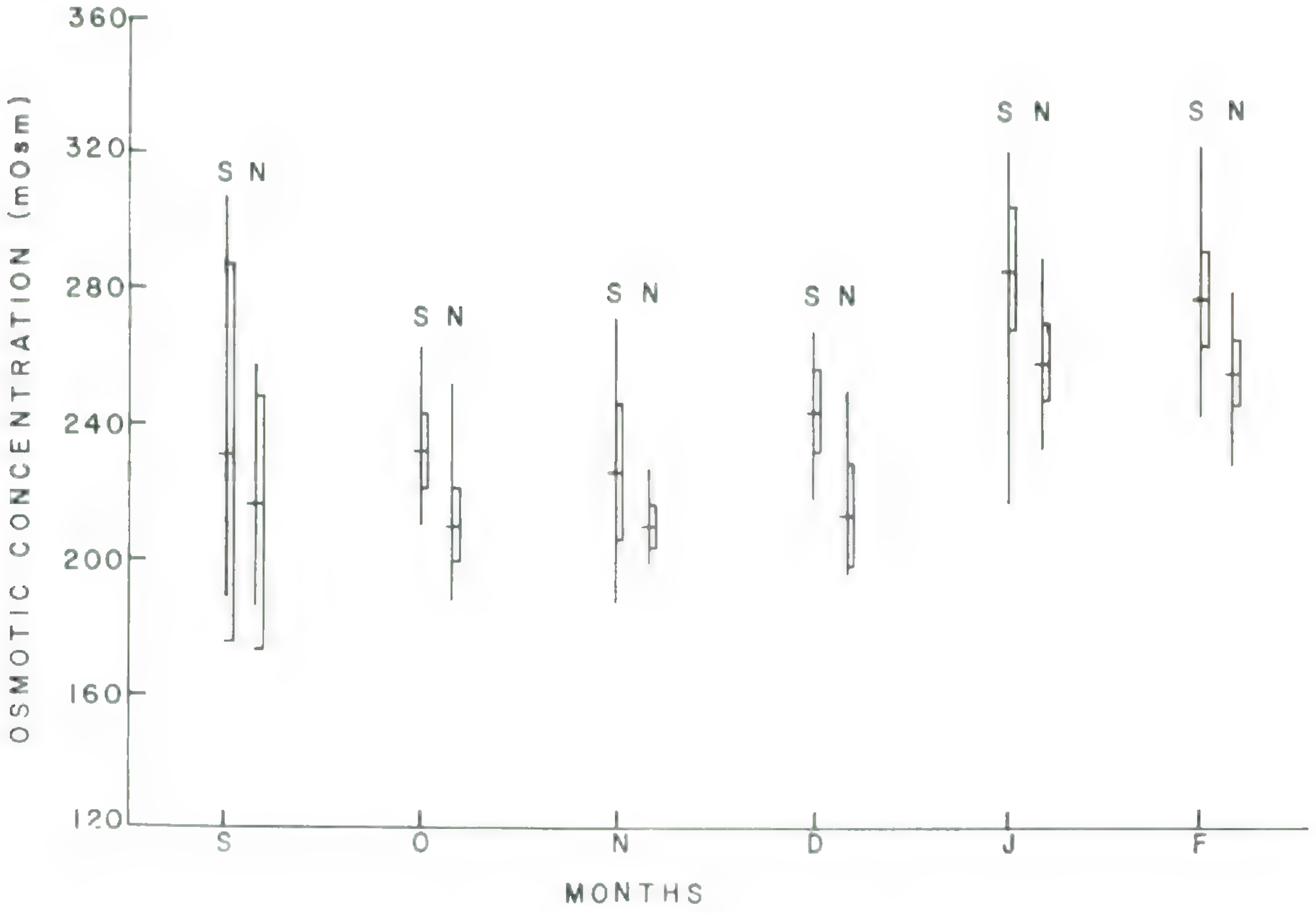

FIGURE 42.—Southern Arizona. Change in osmotic concentration of cortex tissue fluids for sahuaro populations at the sampling sites on the bajadas of the Tucson Mountains and Santa Catalina Mountains (foothill and 817 meter sites), Tucson, Pima County, Arizona, fom September 1966 to February 1967. Frequency distributions graphed for the osmotic concentrations on the south (S) and north (N) sides of the sahuaros.

In February at the northern end of the geographic range the osmotic concentration of sahuaro cortex fluids showed on increase. This followed the cessation of the winter rains (January) in the area, and at this time the concentration on the south sides of the plants became significantly higher ($P < .001$) than that of the north. The significant difference between the south and north coinciding with a period of decreased or minimal rainfall was similar to the long term responses found in southern Sonora (November 1966–February 1967) and at Tucson, Arizona (October 1966–February 1967).

The concentration of plant tissue fluids on the north and south sides of the sahuaro cactus were influenced by the regional precipitation. There was no significant difference in the osmotic concentration between the north and south sides of the plants following periods of extensive effective precipitation. This occurred at all sites along the cline monitored in this study. The effect of the high amount of precipitation of one month may carry over into the next, damping any significant difference between south and north (December–January, northern Arizona).

During periods with little or no effective precipitation the concentration of the south sides of a sahuaro became significantly higher than that of the north. This was a result of the net water loss being greater on the south sides of the plant due to the microclimatic conditions, *e.g.*, higher tissue temperatures on the

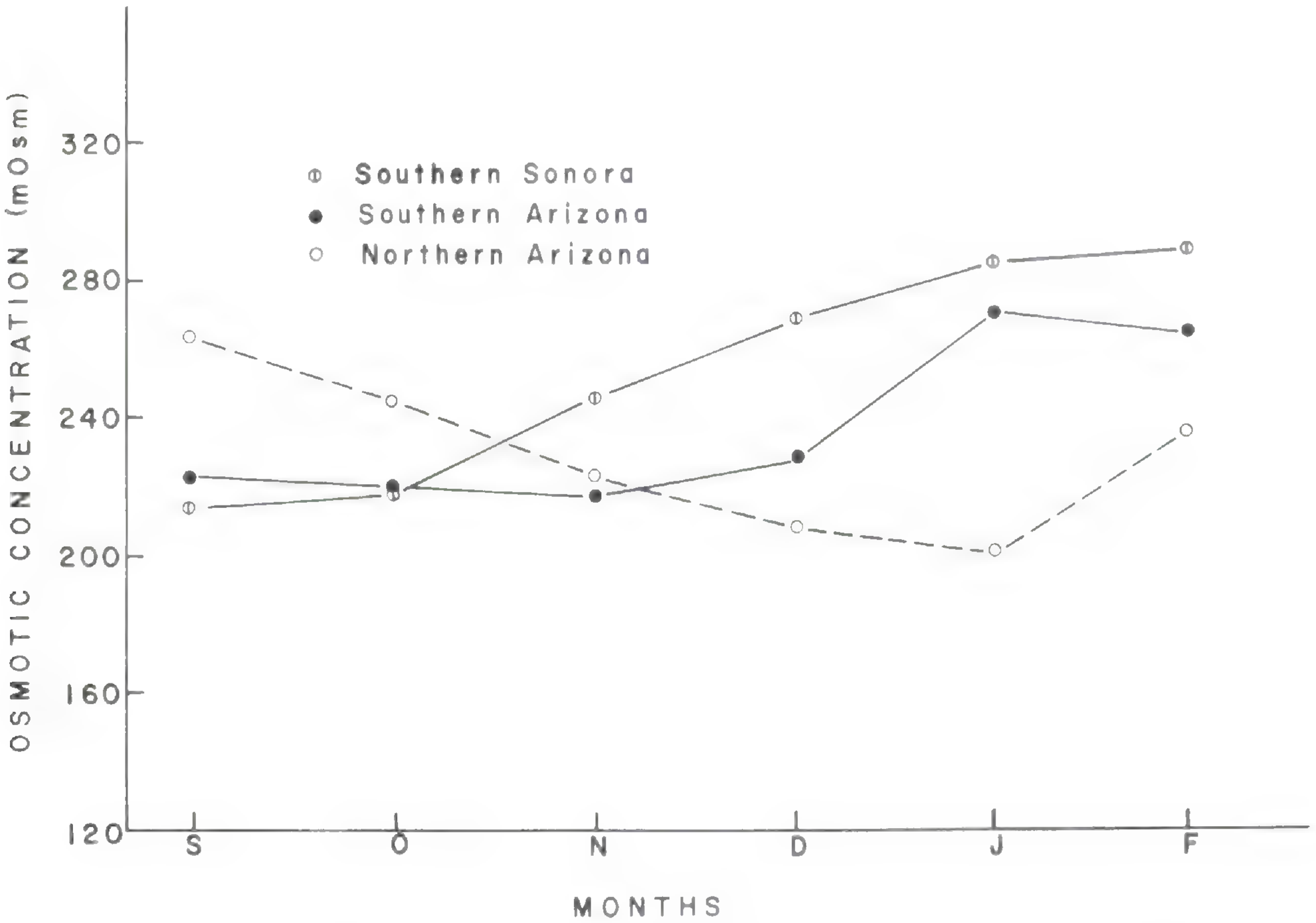

FIGURE 43.—Change in mean osmotic concentration (mOsm) for all monitoring sites in southern Sonora, northern Arizona, and the lower and middle bajada sites in southern Arizona from September 1966 to February 1967. Hatched circles, southern Sonora; closed circles, southern Arizona; open circles, northern Arizona.

south sides, and physiological responses, *e.g.*, increased transpirational water loss.

The significantly higher concentration on the north sides of the sahuaros in northern Arizona during November 1966 suggests a potential hardiness which was diluted the following month by the heavy December rains. This occurred in the face of continuing hydration by the plants which normally leads to no significant difference between the two sides. Since the first temperatures below 0° C in the observed range of the sahuaro occurred during this period in this region, a physiological response to this cold-stress can be anticipated.

Two *t* tests (for frequency distributions and for paired comparison analysis) were used to determine significance of differences in the osmotic concentration between the south and north sides of the sahuaro cacti sampled. The results of these two tests were similar in all cases but four. In these four cases the sensitivity of the paired samples comparison showed significant differences (February, southern Sonora; November, Tucson; November and February, northern Arizona) which did not appear significant through graphing by the Dice-Leraas method. The two November differences were associated with the first freeze of the winter, and specifically in northern Arizona showed a tendency for increased concentration on the north side.

Elevational Concentration. The elevational transect on the Santa Catalina Mountains, monitored for changes in osmotic pressure of sahuaro cortex fluids, follows the Catalina Highway from the lower bajada (817 m) to the upper limits

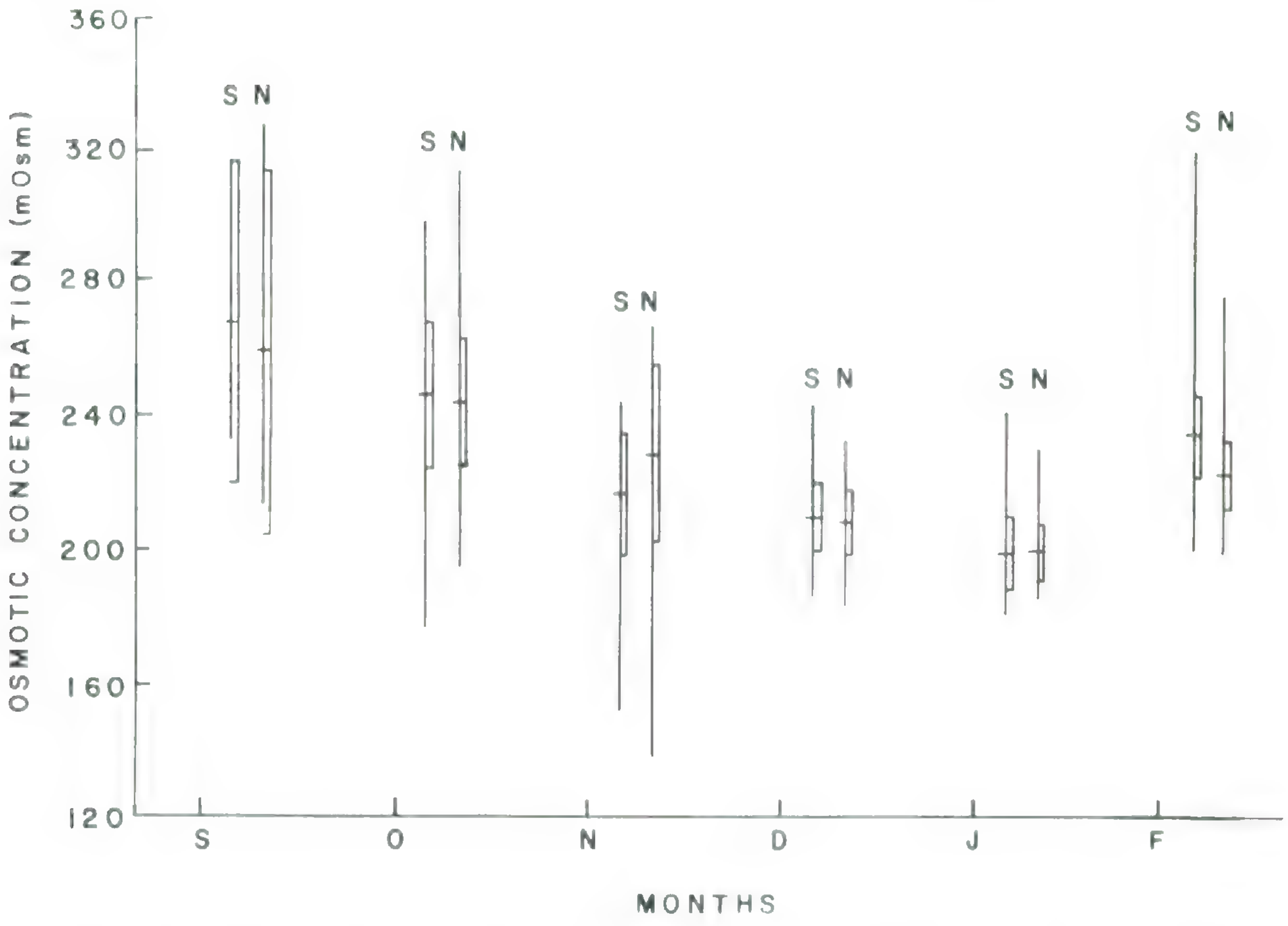

FIGURE 44.—Northern Arizona. Change in osmotic concentration (mOsm) of sahuaro cortex tissue fluids for all monitoring sites in northern Arizona from September 1966 to February 1967. Frequency distribution graphed for osmotic concentrations on the south (S) and north (N) sides of the sahuaros.

of easily accessible sahuaros (1317 m). The lower bajada supports desertscrub communities characterized primarily by creosotebush (*Larrea divaricata*). The uppermost sahuaros are in a grassland-woodland transition, where amole (*Agave schottii*) and Emory oak (*Quercus emoryi*) are conspicuous (see Habitats). All five stations along this transect showed significant ($P < .05$) increases in osmotic concentration through the six-month period of monitoring. As elsewhere in the Tucson region as in southern Sonora, the lower initial readings followed the wet summer and the increased osmotic values found at all sites were related to the subsequent reduction of plant-available moisture.

The decrease in osmotic pressure with increasing elevation along the transect became more pronounced as the winter progressed. Initially (September) there was no significant difference ($P > .05$) between the concentrations on the south and north sides of the sahuaros along this gradient. And at this time the relationship between change in osmotic pressure and change in elevation was not clear. However, when the difference between the concentrations on the south and north sides became significant ($P < .05$) during and after November, a relationship between the concentration and the elevation became apparent for the south sides of the sahuaros (see ordering in Table 16).

Starting in November, and continuing for the remainder of the six-month monitoring period, the concentation on the south sides of the sahuaros at the

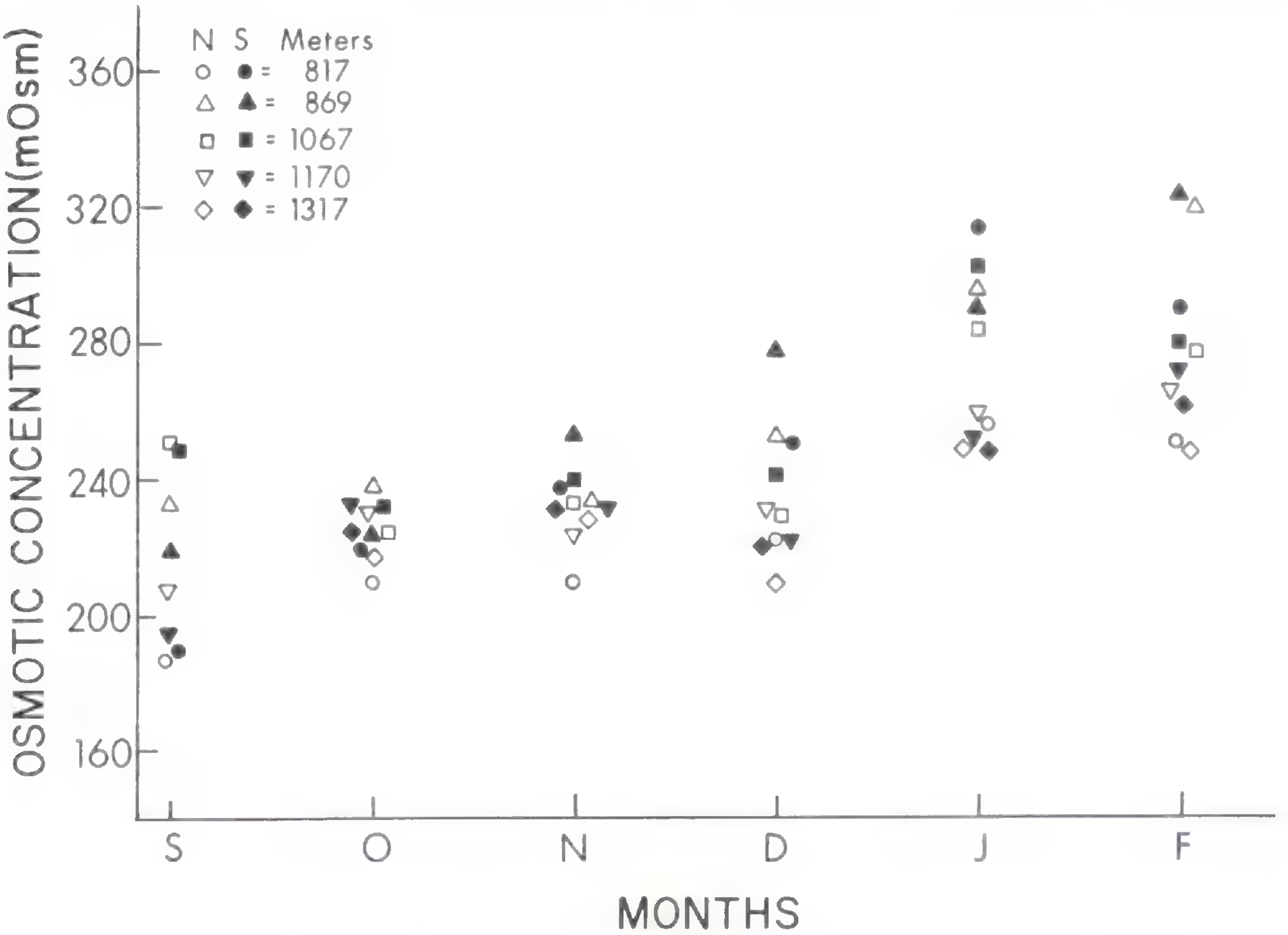

FIGURE 45.—Order of sahuaro tissue fluid monitoring sites on the Santa Catalina elevational transect by ranking of mean osmotic pressure on south side (closed symbol) and north side (open symbol) from September 1966 to February 1967. Circle, 817 meter site; triangle, 869 meter site; square, 1067 meter site; inverted triangle, 1170 meter site; diamond, 1317 meter site.

lowest elevation (817 m) was the most or second most concentrated found at all the stations on the transect. Moreover, the highest two sites (1170 m and 1317 m) had the lowest osmotic concentrations (minimum resistance to freezing), and the top site was the most dilute throughout the period (Table 16, Fig. 45).

On the north sides of the plants there was also a relationship between the concentration and elevation. From December through February the osmotic pressure decreased with increasing elevation at all sites with the exception of 817 m, the cactus fluids of which were unusually low in concentration throughout the monitoring period. Only in November was there any reversal of the general order of decreasing osmotic concentration with increasing elevation on the north sides of the sahuaros. This was also the month in which the first freezing temperatures of the winter of 1966–67 were recorded (see Climate and Weather).

In summary, there was no significant difference in the concentration between the south and north sides of the sahuaros along the transect when they were in an advanced state of hydration. With the cessation of large amounts of effective precipitation, net water losses led to an increasing of osmotic pressure of the sahuaro cortex tissue fluids. By November this increase had resulted in a significant difference between the south and north sides of the sahuaros on this elevational gradient. Also by November a significant difference had developed between the

TABLE 22. Extreme low temperatures and monthly mean minimum temperatures for the monitoring period at representative stations along the latitudinal transect through the geographic range of the sahuaro (September 1966 February 1967).

Site	Low extreme, ° C	Monthly mean minimum, ° C
Navojoa, Sonora	+3.0, 30 Dec.	+8.7, Jan.
Tucson International Airport	6.7, 7 Jan.	+2.0, Jan.
University of Arizona, Tucson	6.7, 8 Jan.	−1.0, Jan.
Tucson Magnetic Observatory	10.0, 7 Jan.	−1.8, Jan.
Wikieup, Arizona	6.7, 27 Dec.	+0.4, Jan.

upper and lower sites on the transect. From this time through the remainder of the six-month monitoring period (February), the osmotic concentrations of the plants at the upper limit (1317 m) were significantly lower than those on the upper bajada (869 m) at the base of the mountains. The cause of this differential dehydration was related to the water factors associated with increased elevation, *e.g.*, reduced evapo-transpiration, reduced temperature, and increased precipitation.

The demands for water by the sahuaros were of similar nature at each site along the gradient as evidenced by the significant increase in concentration through the monitoring period and the higher osmotic pressure on the south side as compared to the north. However, the demands were not as strong as shown by the significantly lower concentrations found at the higher elevations. This reduction of osmotic pressure in response to greater plant-available soil moisture, even in the face of lower environmental temperatures, was similar to the response of the sahuaros in northern Arizona to the winter rains of 1966.

CLIMATE AND WEATHER

Southern Sonora has higher winter temperatures than northern Arizona. The difference of approximately 8 degrees of latitude between the northern and southern limits of the sahuaro and the more continental position of the northern end of the range account for the difference in the winter temperatures between the sites from southern Sonora to northern Arizona. With regard to extreme temperatures, the higher temperatures due to the continental position of the northern end of the range (Mohave County, Arizona) outweighs the influence of the difference in latitude to lower the temperature and the summer temperatures are uniformly high along this north-south cline from southern Sonora to northern Arizona (Shreve, 1951; Smith, 1956; Lowe, 1967*a*).

The entire range of the sahuaro has a bi-seasonal precipitation pattern. The summer rains are usually due to thunderstorms that are local in nature and short-lived. Summer storms are a result of solar heating of the air and its subsequent rise, condensation, and fall in the form of precipitation occasionally with hail. The moisture source for this is supplied by moist tropical air currents from

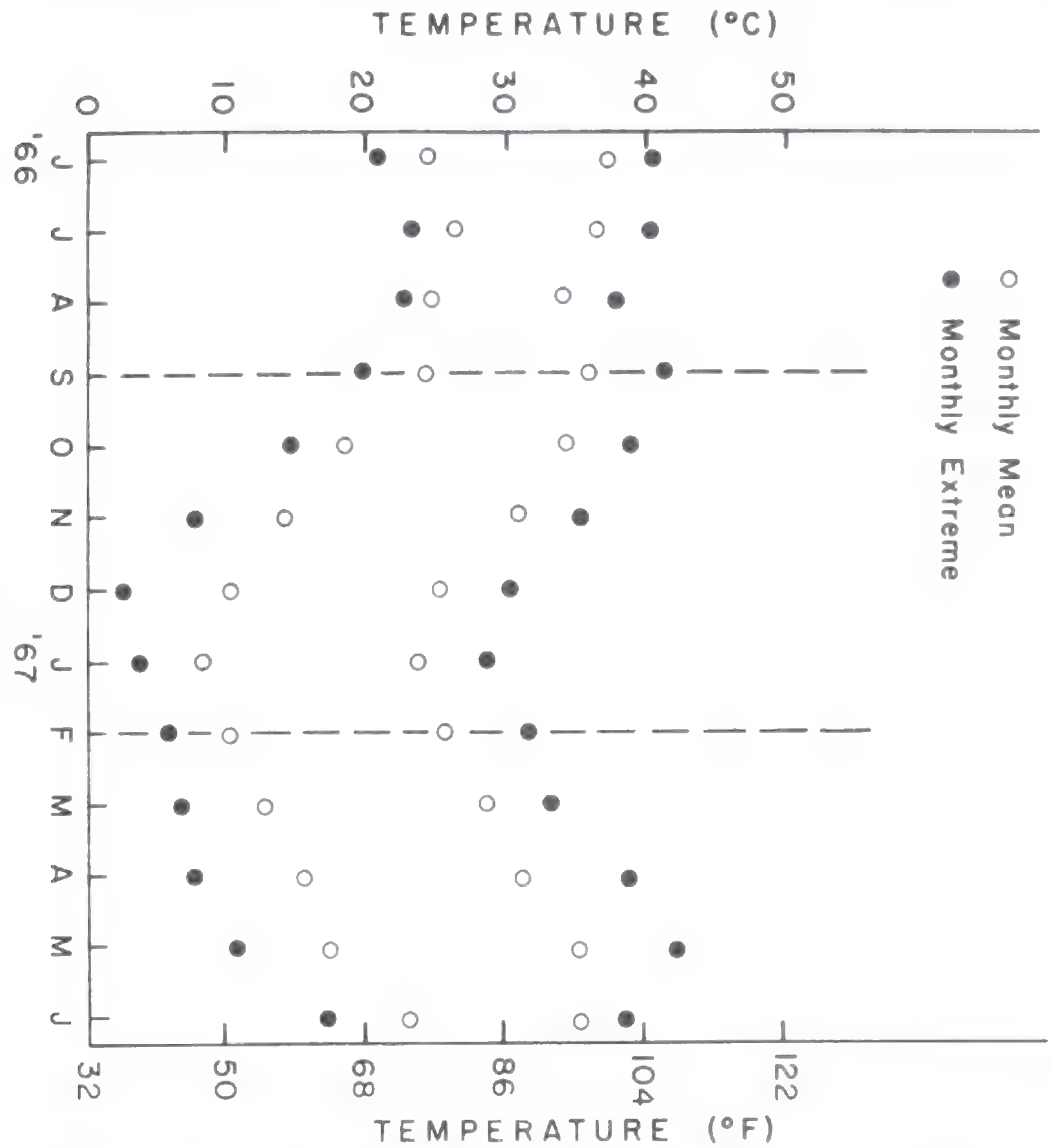

FIGURE 46. Navojoa, Sonora, Mexico. Extreme monthly maximum and minimum temperatures (closed circles) and mean monthly maximum and minimum temperatures (open circles). June 1966 to June 1967. The period of monitoring is indicated by dashed lines.

the southeast and southwest. The winter rains are generally gentle showers, often of several days duration. The winter precipitation results from activity on the Pacific polar front to the northwest (Smith, 1956; Lowe, 1967*a*).

TEMPERATURE

The seasonal amplitude of temperature in the range of the sahuaro is one of the greatest of any of the giant cacti. In the Sonoran Desert the northern stations show slightly higher maxima during the summer and lower minima during the winter than do the southern stations (Shreve, 1951). The representative weather stations, as graphed in Figs. 46–48, support this for the period of monitoring during the winter of 1966–67 and the summer prior to the period of monitoring.

TABLE 23. Monthly mean temperatures for the 13 month period (June 1966–June 1967) bracketing the period of monitoring and the average monthly mean temperatures for the Wikieup, Mohave County, Arizona station from 1952-1962. Data from Department of Commerce (1966*a*, 1967*a*).

Date	Monthly mean temperature, June 1966–June 1967	Average monthly mean
1966		
June	26.7° C (80.0° F)	26.7° C (80.0° F)
July	30.5° C (86.9° F)	30.4° C (86.7° F)
August	30.9° C (87.6° F)	29.4° C (84.8° F)
September	26.9° C (80.3° F)	26.1° C (79.0° F)
October	19.6° C (67.3° F)	20.2° C (68.3° F)
November	14.2° C (57.6° F)	13.5° C (56.3° F)
December	9.9° C (49.8° F)	9.9° C (49.8° F)
1967		
January	10.0° C (49.9° F)	9.1° C (48.3° F)
February	12.4° C (54.3° F)	10.3° C (50.6° F)
March	14.5° C (58.1° F)	12.5° C (54.4° F)
April	13.0° C (56.4° F)	17.2° C (63.0° F)
May	21.7° C (71.1° F)	21.1° C (70.0° F)
June	25.2° C (77.3° F)	26.7° C (80.0° F)

Low temperature is most limiting to tropical and subtropical species at the upper elevational limits of the range of the species (Thornber, 1910; Lowe, 1967*a*). This ability to function at low temperatures is also important in the latitudinal distribution of the species. In the eastern, northeastern, and northern portions of the range of the sahuaro, low winter temperatures play a very important role in setting the geographical limits for the species.

Southern Sonora. The coolest month of the year at Navojoa, Sonora, Mexico, is January with a mean monthly temperature of 18° C (Secretaria de Recursos Hidraulicos, 1952; Hastings, 1964). Official weather records from 1962 through the summer of 1967 (Fig. 46, Table 17) show January and February have the lowest extreme temperatures and the lowest mean monthly minimum values. Freezing temperatures are rare and snow is almost totally absent. Frost (helada) is recorded infrequently during January and February (eight days in January 1963). Its effect is minimal and not entirely clear considering the essential lack of reported freezing temperatures.

Based on a comparison of mean monthly temperatures, the summer before the sampling began (June, July, and August 1966; Table 18) was not significantly different in temperature from the expected ($P > .05$). During the monitoring period (September 1966 February 1967; Table 18), the temperatures were below the mean or equal to it for each month, based on weather records from 1922–1962. However, the difference is not significant ($P > .05$).

The monthly extreme temperatures for the past five years and the monthly mean temperatures for 40 years, based on weather bureau information, show the temperatures at the monitoring sites in southern Sonora during the period of

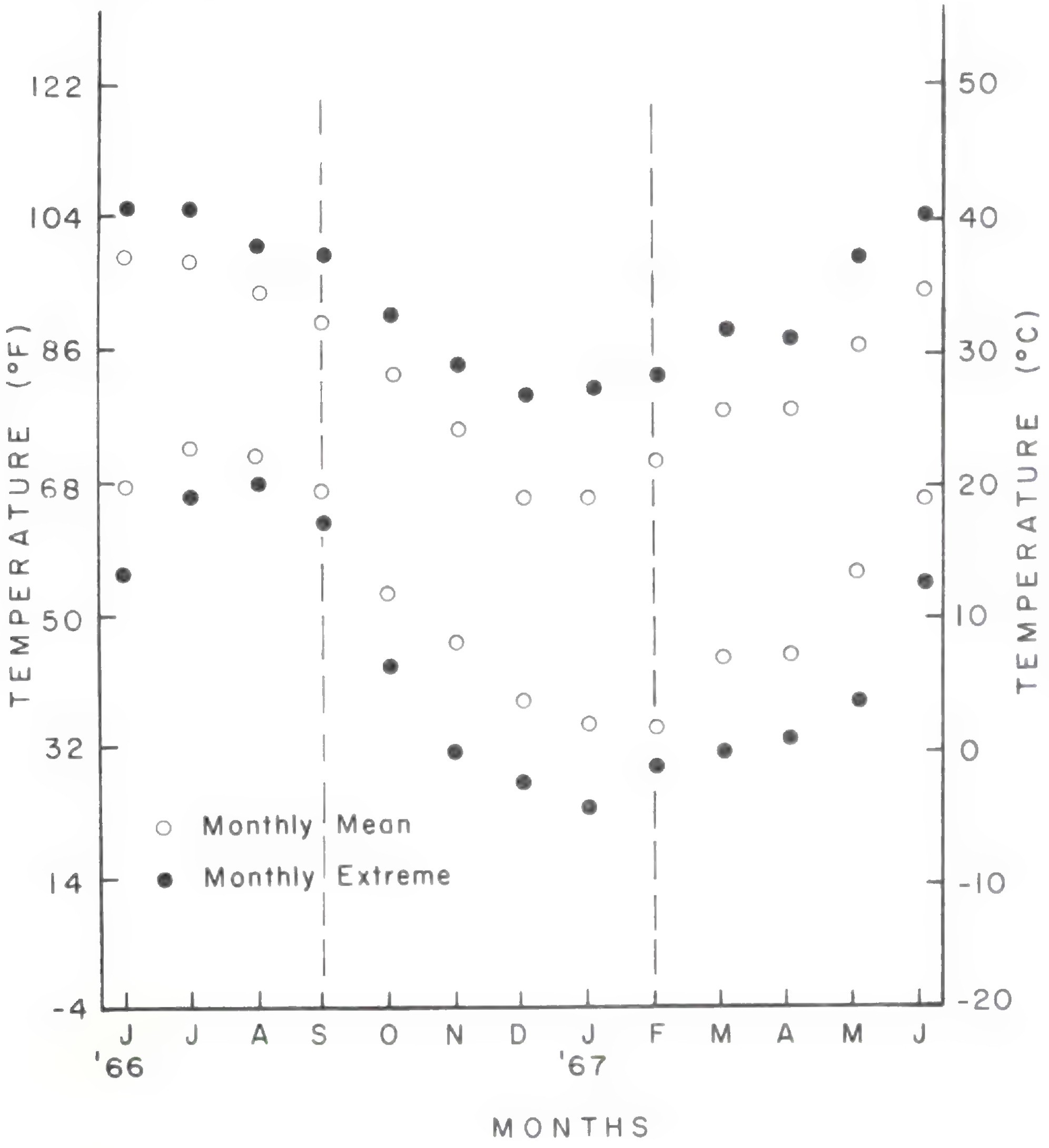

FIGURE 47.—Tucson, Pima County, Arizona. Extreme monthly maximum and minimum temperatures (closed circles) and mean monthly maximum and minimum temperatures (open circles). Data from Tucson International Airport, June 1966 to June 1967. The period of monitoring is indicated by dashed lines.

sampling to be moderate with values near or below the mean, but not significantly different from the mean.

Southern Arizona. As at Navojoa, the coldest month of the year in Tucson is January and the warmest is July (Fig. 47, Tables 19–20). The temperature of the summer and late-summer period preceding and during the sampling of the sahuaros was not significantly different than the expected ($P > .05$); while the winter and late-winter of the observation period had temperatures above normal, but not significantly different ($P > .05$) than the anticipated based on mean monthly temperatures (Table 19).

The low winter minimum temperatures for the period of monitoring were not significantly different than the normal for this period ($P > .05$). Moreover, the extreme temperatures did not approach record lows during any of the months (Table 20). Thus the winter of 1966–67 here, as in southern Sonora, was moderate even though there were 20 days with temperatures of 0° C or below. Nine of the 20 days were consecutive—December 27 to January 4.

Northern Arizona. The amplitude of seasonal temperatures at the weather station in Wikieup, Arizona, was broad (53° C). Wikieup was warmer than the other stations on the latitudinal transect during the summer prior to monitoring. The extreme (43.9° C (111° F), 5 August 1966) and the average monthly maximum (40.2° C (104.3° F), July 1966) were slightly higher than at the southern recording station at Navojoa, Sonora (41.5° C and 36.0° C). The extreme and mean monthly maximum were also higher at Wikieup than at the official recording station at the Tucson International Airport (40.5° C and 36.8° C) and above those at the University of Arizona (Tucson) station (42.8° C and 39.6° C) and the Tucson Magnetic Observatory (41.1° C and 37.8° C) (summarized in Table 21).

The low temperatures during the period of observation were extreme at the northern end of the range of the sahuaro. There were 16 consecutive days with minimum temperatures of 0° C or below during December and January. This is more than at any official recording station in Tucson (12 consecutive days at the University of Arizona and 9 consecutive days at the Tucson International Airport).

The extreme minimum temperature (−6.7° C (20° F), 27 December 1966) and the lowest average monthly minimum (−0.4° C (34.4° F) January 1967) were below those for the Tucson International Airport (Table 22). However, both the University of Arizona and the Tucson Magnetic Observatory recorded data for January means below that for Wikieup, while the extreme low readings at the University matched Wikieup, and the extreme minimum temperature at the Magnetic Observatory was below that of the Wikieup station (Table 22).

The mean temperatures and extreme temperatures at the Wikieup weather station during the period of monitoring (September 1966–February 1967) were higher than normal, but this was not significant ($P > .05$; Tables 22–23, Fig. 48).

PRECIPITATION

Southern Sonora. This analysis is based on the data obtained at Navojoa, Sonora, Mexico. Navojoa is located in the arid subtropical scrub of coastal northwestern Mexico and has a distinctive bi-seasonal precipitation pattern (Fig. 49, Table 24). As in Tucson and southern Arizona, the summer precipitation contributes the greatest percentage to the total annual precipitation. At Navojoa the summer rains provide 47.5% (July and August) to 68.8% (July, August, and September) of the total annual precipitation; additional summer rain falls in June and in October. The winter rains (December–March) amount to only 17.4–18.4% of the total (Table 24). The higher overall precipitation here does not

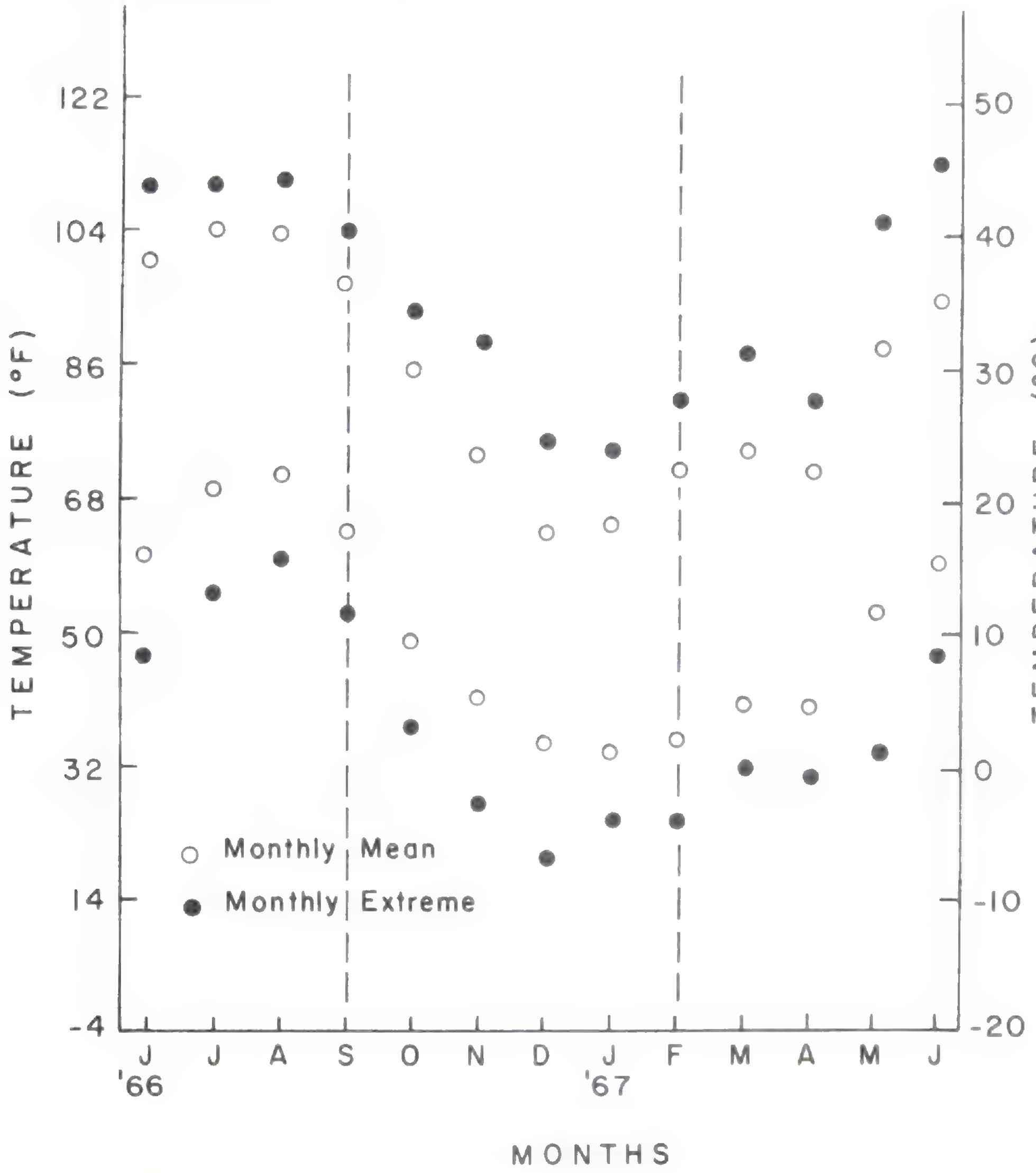

FIGURE 48.—Wikieup, Mohave County, Arizona. Extreme monthly maximum and minimum temperatures (closed circles) and mean monthly maximum temperatures (open circles). June 1966 to June 1967. The period of monitoring is indicated by dashed lines.

outweigh the lower winter percentage. Thus both the percentage and the total of the winter rainfall is reduced at the southern geographic limit of the sahuaro.

The three summer months of June, July, and August 1966 prior to the period of monitoring were significantly ($P < .001$) wetter than normal. This included August, the month immediately prior to the period of sampling; it is generally the wettest month of the year. August 1966 had more than twice the average amount of rain—93.9 mm (3.7 inches) *versus* 201.4 mm (7.93 inches). This made it the second wettest August on record at Navojoa. Following the extremely heavy August rains, the precipitation pattern followed the normal curve, but at

TABLE 24. Seasonal distribution of precipitation for selected points in the geographic range of the sahuaro. Observed values presented for the period of June 1966 May 1967 and mean values (in parentheses) based on official weather records for each recording station.

Site	Summer, per cent total annual		Winter, per cent total annual		Total (inches/mm)
	July–Aug.	July–Sept.	Dec.–Feb.	Dec.–March	
Navojoa, Sonora	72.5%	90.0%	3.9%	3.9%	16.09/408.7
	(47.5%)	(68.8%)	(17.4%)	(18.4%)	(15.06/382.5)
Tucson Airport	51.2%	81.9%	3.1%	6.7%	11.49/291.8
	(38.8%)	(59.0%)	(23.4%)	(29.5%)	(10.69/271.5)
Tucson Magnetic Observatory	39.9%	72.0%	3.4%	7.4%	11.85/301.0
	(36.5%)	(45.6%)	(27.6%)	(35.1%)	(11.54 293.1)
Wikieup, Arizona	2.0%	19.9%	35.9%	46.2%	6.54/166.1
	(25.2%)	(34.1%)	(36.9%)	(45.9%)	(10.49/266.4)

amounts significantly ($P < .001$) below the normal for Navojoa (Fig. 49). In a period of 267 days between the end of September 1966 and the end of June 1967, there was only one day of effective precipitation, 31 December 1967 (15 mm (0.59 inch)).

Southern Arizona. The Tucson region had a wet summer, followed by a very dry winter in 1966–67 (Table 24). As at Navojoa the summer precipitation here was significantly above the normal ($P < .001$) during the summer of 1966 (June, July, August, and September). This was climaxed by a September total that was 350% of the normal for the month (Fig. 50, Table 25). However, the winter rainfall (December–March) was significantly below normal ($P < .001$), being only 14% of normal for the remainder of the period of sampling—0.74 inches (18.8 mm) *versus* 3.84 inches (97.5 mm).

The bi-seasonal rainfall pattern a Tucson is dominated by the summer precipitation, which is not much greater than the winter in percentage of the total. Approximately 35–60% of the total annual normally falls within this period during July, August, and September (Table 24). In 1966–67 the reduced amount of winter precipitation swelled the percentage for the summer rains to 51–82% (Fig. 50, Table 24). The winter rainfall picture is different from that of the summer. The total precipitation for December, January, February, and March as a percentage of the annual precipitation decreases to approximately 20–35%. In the winter of 1966–67 this percentage decreased to 3–7% (Table 24).

Northern Arizona. The occurrence of higher than average precipitation during the summer prior to the period of observation at Navojoa and at Tucson did not occur at Wikieup, Arizona. Here the summer rains of June, July, and August 1966 failed to appear (Table 24), while the fall and early winter precipitation (September, October, November, and December 1966) was significantly ($P < .001$) above normal (Fig. 51). December, instead of August as expected, was the wettest month during the period of observation at Wikieup. December 1966 was followed by a period of below normal precipitation which lasted into the summer of 1967.

The northern end of the range of the sahuaro normally has a rainfall pattern characterized by two peaks, August and February. The latter represents the winter rains which dominate the seasonal rainfall pattern (Table 24, Fig. 51), in contrast to Tucson or Navojoa where the summer rains dominate the annual precipitation distribution. Normally August is the wettest month of the year throughout the range of the sahuaro. However, in 1966 less than one tenth of the expected precipitation fell—0.15 inch (3.8 mm) *versus* 1.70 inches (43.2 mm)—at the recording station at Wikieup, Arizona. Also February, normally the second wettest month at the northern end of the distribution of the sahuaro, had no rain as compared to an expected 1.3 inches.

Wikieup was also the only recording site to receive measurable amounts of snow during the period of monitoring. There were six days in December 1966 with snow of more than 0.1 inch. The total amount of snow for this period was 1.0 inch. A comparison of values shows that Tucson International Airport receives an average of 1.4 inches of snow annually almost equally distributed from

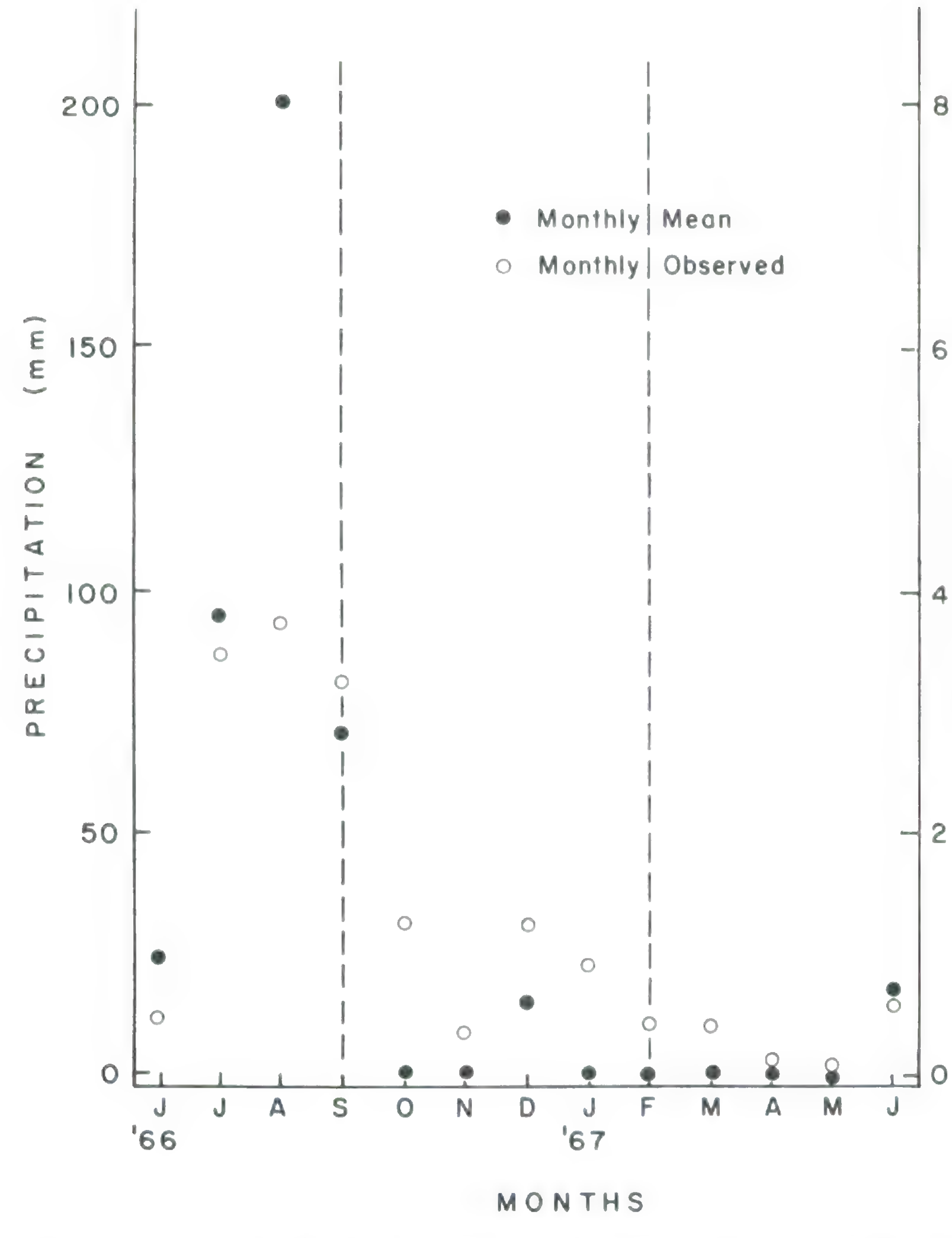

Figure 49.—Navojoa, Sonora, Mexico. Monthly precipitation (closed circles) for June 1966 to June 1967, and mean monthly precipitation (open circles) based on official weather records from 1922–1962. The period of monitoring is indicated by dashed lines. August 1966 was the second wettest August on record.

November through March, while Wikieup receives an average of 0.3 inch annually.

In summary, monthly temperatures at all sites monitored for change in sahuaro cortex fluid osmotic pressure were not significantly different from the expected, prior to and during the period of sampling.

TABLE 25. Monthly total precipitation for the 13 month period (June 1966–June 1967) bracketing the period of monitoring, mean monthly total precipitation, and record maximum precipitation, for Tucson International Airport, Pima County, Arizona

Date	Monthly total, inches(mm)	Mean monthly total, inches(mm)	Record maximum, inches(mm), date
1966			
June	0.02(0.5)	0.29(7.4)	1.46(37.1), 1954
July	2.57(65.3)	2.06(52.5)	5.20(132.1), 1958
August	3.31(84.1)	2.88(73.2)	7.93(201.4), 1955
September	3.53(89.7)	1.00(25.4)	5.11(129.8), 1964
October	0.32(8.1)	0.64(16.3)	2.62(66.5), 1957
November	0.06(1.5)	0.62(15.7)	1.90(48.3), 1952
December	0.19(4.8)	0.92(23.4)	5.02(127.5), 1965
1967			
January	0.04(1.0)	0.82(20.8)	2.37(60.2), 1957
February	0.13(3.3)	0.84(21.3)	2.27(57.7), 1941
March	0.41(10.4)	0.53(13.5)	2.26(57.4), 1952
April	0.29(7.4)	0.27(6.9)	1.66(42.2), 1951
May	0.62(15.8)	0.13(3.3)	0.89(22.6), 1943
June	0.42(10.7)	0.29(7.4)	1.46(37.1), 1954

There were highly significant differences from the expected in the amounts of precipitation at all of these sites. In southern Sonora and southern Arizona, the precipitation of summer months (June, July, and August) prior to sampling was in significantly higher amounts than normal. This was followed by significantly reduced fall and winter precipitation (September–February). In northern Arizona, the reverse was true. The expected summer rains for June, July, and August essentially did not appear, and precipitation for the first part of the sampling period (September–December) was significantly heavier than normal. In late winter, the precipitation ceased and conditions of below normal precipitation carried on from late winter into the following summer.

SUMMARY

Changes in osmotic concentration of sahuaro cortex tissue fluids were monitored on a latitudinal transect from southern Sonora into northern Arizona and on an elevational transect to 1317 m in the Santa Catalina Mountains in southern Arizona. The determination of physiological change along these complex environmental gradients provided information linking physiological adjustment and genetic adaptation of the sahuaro to its effective environments.

Resistance to the effects of low environmental temperature, as indicated by change in the osmotic pressure of the tissue fluids, was influenced more by seasonal effective precipitation than by seasonal temperature within the limits of the sensitivity and timing of these tests.

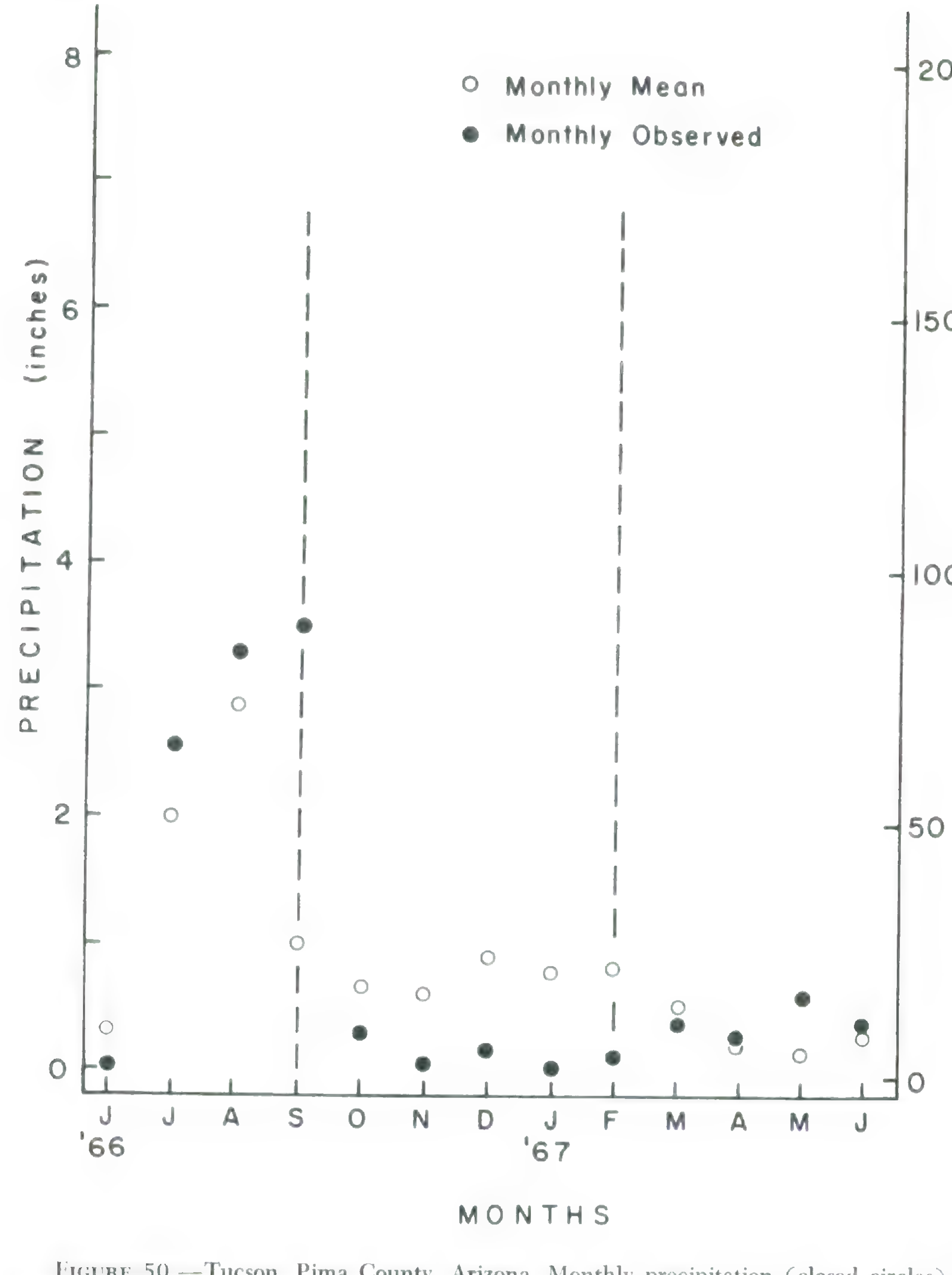

Figure 50.—Tucson, Pima County, Arizona. Monthly precipitation (closed circles) for June 1966 to June 1967 and mean monthly precipitation (open circles) based on official weather records from 1940 1966. The period of monitoring is indicated by dashed lines.

The summer environmental temperatures are uniformly high throughout the range of the sahuaro. There was no significant difference from the expected temperatures prior to the period of monitoring the osmotic pressure (June, July, and August 1966). There were also no significant differences in either this pattern

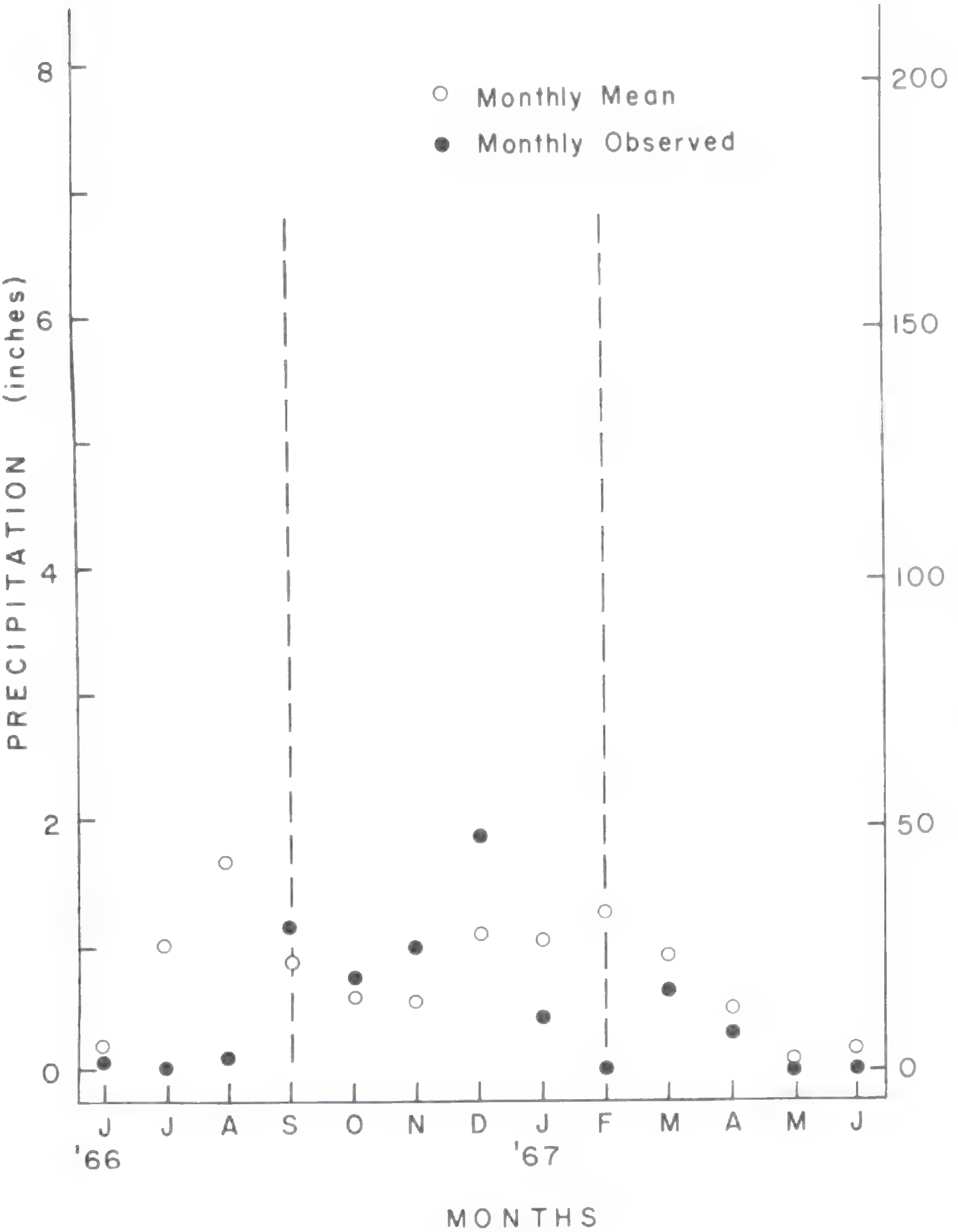

FIGURE 51.—Wikieup, Mohave County, Arizona. Monthly precipitation (closed circles) from June 1966 to June 1967 and mean monthly precipitation (open circles) based on official weather records from 1925–1966. The period of monitoring is indicated by dashed lines.

or the expected temperatures during the period of fall and winter monitoring (September 1966–February 1967). There is a gradient in the winter temperature

from low ambients below freezing at the northern end of the range of the sahuaro (northern Arizona) to higher winter temperatures at the southern end of the range (southern Sonora).

There is ordinarily an increase in the amount of seasonal precipitation from north (northern Arizona) to south (southern Sonora) throughout the range of the sahuaro. There is also a marked shift in the annual precipitation pattern, which is dominated by winter rains in the north and by the summer rains toward the southern end of the range of the sahuaro in southern Sonora. Prior to the monitoring period in southern Sonora and southern Arizona, the amount of precipitation was significantly higher than normal, while in northern Arizona the precipitation prior to monitoring was significantly below normal. However, during the period of sampling, the rainfall in southern Sonora and southern Arizona was significantly less than normal. In northern Arizona it was significantly wetter than expected until the end of the monitoring period when the precipitation ceased.

The sahuaros in southern Sonora and southern Arizona showed significant increases in osmotic concentration from low values in September to high ones in January and February at the population level. This paralleled decreased availability of water and decreasing seasonal temperatures. In northern Arizona there was a significant decrease in the concentration of the osmotic pressure of sahuaro cortex fluids paralleling the increase in the availability of water. This resulted in the lowest osmotic concentrations coinciding with the lowest seasonal temperatures at some sites. The osmotic concentration rose significantly in February following a period of no precipitation.

During the winter, decreasing osmotic pressure was found to parallel increasing elevation along the elevational transect on the Santa Catalina Mountains, near Tucson, Arizona. This follows a pattern of osmotic concentration, as an indicator of resistance to low temperature, being more sensitive to available moisture than to low temperature.

The point of maximum hydration, *i.e.*, minimum osmotic concentration, was uniform throughout the geographic range of the sahuaro. This suggests a genetically fixed adaptive limit. The point of maximum osmotic concentration was not observed since the environmental parameters determining this point, high temperature and lack of precipitation (see below), were neither extreme nor uniform during the period of monitoring.

As the point of maximum hydration was approached the concentration of the cortex tissue fluids on the south and north sides of the sahuaro neared equal values. The south sides of the plants were more sensitive, *i.e.*, they reacted more quickly as indicated by changes in osmotic concentration. The south side increased in concentration more rapidly and decreased more rapidly than the north. The higher tissue temperatures on the south sides of the sahuaros accounts in part for this greater sensitivity. The difference in concentration between the higher values on the south sides and the lower comparable values on the north sides was significant during periods with no effective precipitation, but this difference was not significant during periods with extensive effective precipitation.

Certain irregular phenomena, such as the osmotic pressure of the north side

being significantly greater than the south side at the time of the first freezing temperatures of the season in the Wikieup area, and higher osmotic concentrations than expected in January in Tucson, suggest a genetically controlled hardiness factor that may be commonly diluted by winter precipitation. The detection of such a factor, in the sense of accurately parcelling the variation, is beyond the sensitivity of the technique used in this study.

The decreasing osmotic pressure of sahuaro cortex tissue fluids and the presence of increasing effective precipitation contribute to the limiting situation at both the northern geographic limit and the upper elevational limit of the sahuaro.

Under the conditions of reduced osmotic pressure and low environmental temperature, the sahuaros are more susceptible to cold damage. There conditions exist at the northern end of the range of the sahuaro (Wikieup, Arizona) where the winter rainfall dominates the annual precipitation and unusually low seasonal temperatures for sahuaros are of regular occurrence. Similar conditions exist at the upper elevational limits of the sahuaro, in the Santa Catalina Mountains near Tucson, Arizona. Here the sahuaros at elevations on the order of 1300–1500 m are subjected to more moisture and lower temperatures than in the desert below. The data are consistent with the hypothesis that low temperature and high moisture coincide in limiting the ecological distribution of the sahuaro at its northernmost localities and at its upper elevational stations.

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TYPE PHOTOGRAPHS OF THE PANAMANIAN COLLECTIONS OF B. C. SEEMANN

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Abstract

Photographs of 132 Panamanian plant collections studied by B. C. Seemann and others for the "Flora of the Isthmus of Panama" are available from the Missouri Botanical Garden. Well over 100 of these collections are possible types.

One of the great achievements of the British Admiralty in the 19th century was the creation of a series of hydrographical and scientific expeditions which have had an enormous and lasting influence on the natural sciences. The most famous of these voyages, which usually came to be designated by the name of the leading ship, was of course that of the H. M. S. *Beagle*. But at least two other expeditions, that of H. M. S. *Sulphur* and that of H. M. S. *Herald*, while of less universal fame, nevertheless, culminated in the production of extensive scientific knowledge. The results of these two expeditions have had a fundamental influence on the treatment of Central American floras due to the large plant collections which were made.

The credit for the first flora of Panama must belong to the naturalist on the expedition of H. M. S. *Herald* (1845–1851), Berthold Carl Seemann (1825–1871), German botanist and indefatigable collector. Several circumstances, one of them an unfortunate accident, coincided to give Seemann the rare opportunity to explore Central America and indeed much of western South America. He re-received his early training at his native town of Hanover and in 1844 went to the Royal Botanic Gardens at Kew to further his botanical studies. Seemann must have impressed Sir William J. Hooker, who in July 1846 recommended him to the British Admiralty as the replacement for Thomas Edmonstone, the original naturalist with H. M. S. *Herald*, who was killed in a gun accident near the Bay of Atacamas, Ecuador.

Seeman arrived at Chagres, Panama, in September 1846 via a West Indian mail packet. At this time the *Herald* was surveying the coastal waters around Vancouver Island, British Columbia. While waiting for the Herald to return, Seemann collected in "Panama" (now the Provinces of Coclé, Colón, Herrera, Los Santos, and Panamá) and "Veraguas" (now the Provinces of Chiriquí, Veraguas, and part of Bocas del Toro). The *Herald* returned to Panama City in January 1847.

Under difficult conditions—heavy rainfall, mosquitoes, and alligators—the *Herald* charted the Bay of Panama until the end of April 1847. At that time the rainfall became so incessant that the ship was forced to return to Panama City. By the first of May the *Herald* was anchored off the island of "Coyba" (Coiba) for the purpose of taking on wood and water, and Seemann added to his collec-

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tions. On 6 May the *Herald* was joined by her tender, H. M. S. *Pandora,* at Iguana Island off Punta Mala, whereupon the two ships sailed southward.

The *Herald* mapped the coast of northwestern South America and returned to the Gulf of Panama (Flamenco Island) on 11 November 1847, where she remained until December first. The ship then began a survey of the coastline between Punta Garachiné (Province of Darien) and the San Juan River (Colombia). On 3 December 1847 a party landed at Punta Garachiné and Seemann collected in the vicinity. He may have also collected near Punta Piña (Province of Darien) since he notes the absence of inhabitants in that area. But he does not specifically state that a party landed. Other collections which Seemann lists as Darien, most specifically the Bay of Cupica (collected 28–31 December 1847), the Bay of Solano, and Cape Corrientes are not Panamanian in contemporary terms, since all are now part of Colombia.

The *Herald* arrived back in the Gulf of Panama in February 1848, and Seemann collected in Panama (*sens. lat.*) and Veraguas (*sens. lat.*) visiting the towns of Chorrera, Natá, Santiago, and David. In May of that year the *Herald* was directed by the British Admiralty to proceed via the Hawaiian Islands to the northwestern coast of North America to assist in the search for the missing expedition of Sir John Franklin and the two ships he commanded, H. M. S. *Terror* and H. M. S. *Erebus.* This was the first of three summer voyages which the *Herald* made (1848, 1849, 1850) in an unsuccessful attempt to find the ill-fated explorers.

The *Herald* returned to Panama in January 1849, was refitted at Taboga Island, and left on 29 January to survey the coasts of Veraguas and Costa Rica. Seemann disembarked at Aguacate Island, went by canoe to Puerto de Remedios, then by horseback to Remedios. From there he proceeded along the beach of Chiru, passing through the villages of San Félix and San Lorenzo, and arrived at David on 14 February. He rejoined the *Herald* at Boca Chica. The expedition then surveyed the waters around "Paredez" (Parida) Island and Point Burica. The *Herald* left Central America on 19 March for the Hawaiian Islands and then turned north on its second trip to Western Eskimaux Land, as Seemann referred to the Arctic regions.

In the fall and winter of 1849–1850 the *Herald* mapped the Gulf of California, and Seemann explored and collected in northwestern Mexico. In the summer of 1850 the ship returned to the Arctic for its third and final endeavor to find evidence or survivors of the Franklin Expedition.

On 30 October 1850 the *Herald* sailed from the Hawaiian Islands on the start of her homeward journey via Hong Kong, Singapore, and the Cape of Good Hope, arriving at Spithead, England, in June 1851.

A narrative of the journey was to have been written by Captain Henry Kellett, who was in command of the *Herald,* but he soon left England to renew the search for the Franklin Expedition. As a result Seemann (1853) published a narrative which, no doubt, because of its broad orientation towards natural history, gives a memorable account of an extensive and remarkable scientific voyage.

Figures 1 2.—Type-photographs of *Eupatorium citronioides* Steetz, number 559* in Seemann's "Synoposis."—1. Entire herbarium sheet. 2. Close-up of inflorescence.

Of greater scientific importance was the publication (with the assistance of specialists in various families) of the "Botany of the Voyage of the Herald" (1852–1857), in which he catalogued and described new taxa from the major areas where he collected. The "Botany of the Voyage of the Herald" consists of: "Flora of Western Eskimaux Land," "Flora of the Isthmus of Panama," "Flora of Northwestern Mexico," and "Flora of the Island of Hong Kong." Even though Seemann and Bedford Pim, an officer on the *Herald,* made an overland journey through Peru and Ecuador during August and September 1847 and presumably collected there, he does not include a flora from that region.

During Seemann's numerous trips in Panama, he collected approximately 1000 specimens, many of which are types.

Through a grant from the American Philosophical Society, the author photographed most of the potential type specimens of the official Seemann study-set (Britten, 1889), which is housed in London at the British Museum (Natural History). "Potential types" refers to those specimens which were the basis for a Latin diagnosis in the "Flora of the Isthmus of Panama" (Seemann, 1852–1857: 57–254).

Some of these specimens could not be found at the British Museum (Natural History) even after searching for them under alternative names. Certain of these missing collections were found and photographed at the Royal Botanic Gardens, Kew. Some could not be located at either institution. This does not deny their existence, of course. While searching for Seemann types, occasionally other Seemann collections, which can not be considered types, were found and photographed. These are also included in the following list.

A 35mm, single-lens reflex camera and panatomic-X film were used. In many instances, *e.g.* specimens with small flowers, a close-up photograph was also taken by means of an E-ring attachment.

The following list of names is organized according to the sequence in the text of Seemann's "Flora of the Isthmus of Panama." The major part of the list consists of taxa treated in the "Synopsis" (Seemann, 1852–57: 74–248), while several species treated in the "Supplement" (Seemann, 1852–57: 249–254) are also included.

Glossy prints of all the photographs are available on loan, by purchase, or through exchange from the Herbarium, Missouri Botanical Garden. All prints are 5 × 7 inches and show the entire herbarium sheet (Fig.1) or details of the plant (Fig. 2). A complete set of prints will be given to the British Museum (Natural History).

The information is listed in the following way. The first number is that used by Seemann in his sequential arrangement of taxa in the text. The name and authority are given exactly as Seemann used them. The collector's name and field collection number are given on the second line of each entry. Seemann rarely cited numbers, and the numbers given here are taken from the specimen sheets. An X in a number designates an unreadable digit. All collections listed as *Seemann s.n.* signify the absence of a collection number on the sheet. The location of the specimen, BM or K, follows the collection number. Occasionally

general comments, *e.g.* conditions of specimens, are given. An asterisk (*) at the end of an entry indicates that a close-up photograph is available in addition to one of the entire sheet.

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Taxa treated in the "Synopsis."

46. PAVONIA ALBA Seem.
Seemann 90 (BM).
64. PACHIRA FENDLERI Seem.
Fendler 310 (BM).*
65. PACHIRA BARRIGON Seem.
Seemann s.n. (BM).
67. ERIODENDRON ANFRACTUOSUM De Cand. var. CARIBAEUM De Cand.
Seemann s.n. (BM).—Three collections on one sheet, two by Sutton Hayes.
82. SLOANEA QUADRIVALIS Seem.
Seemann 1625 (BM).*
85. HELIOCARPUS ARBORESCENS Seem.
Seemann s.n. (BM).*
89. TRIUMFETTA SPECIOSA Seem.
Seemann 1240 (K).
104. HYPERICUM GNIDIOIDES Seem.
Seemann 1640 (BM).*
106. REGGERIA ACUMINATA Seem.
Seemann 1089 (BM).
108. CLUSIA ODORATA Seem.
Seemann 1638 (BM).
109. CLUSIA PRATENSIS Seem.
Seemann s.n. (BM).
CLUSIA—In "undetermined" folder.
Seemann 1639 (BM).—Boquete; sterile specimen.
Seemann s.n. (BM).
113. CALOPHYLLUM CALABA Jacq.
Seemann 1636 (BM).
114. CALOPHYLLUM EDULE Seem.
Seemann 1635 (BM).
123. SALACIA PRUINOSA Seem.
Seemann 1219 (BM).
135. BANISTERIA FERRUGINEA Cav.
Seemann 79 (BM).*
137. TETRAPTERIS CALOPHYLLA Adr. Juss.
Seemann 84 (BM), *1216* (BM).*
138. TETRAPTERIS PANAMENSIS Seem.
Seemann 1215 (BM).*
140. SERJANIA GRANDIS Seem.
Seemann 1643 (BM).*
150. CUPANIA SYLVATICA Seem.
Seemann s.n. (BM).
154. MOSCHOXYLON VERAGUASENSE Seem.
Seemann s.n. (BM).*
168. PICRAMNIA UMBROSA Seem.
Seemann 600 (BM).*
171. CESPEDESIA MACROPHYLLA Seem.
Seemann 1039 (BM).
172. GOUANIA BLANCHETIANA Miq.
Seemann 1647 (BM).*
173. GOUANIA TOMENTOSA Jacq.
Seemann 335 (BM).—In flower.
Fendler 108 (BM).—In fruit.
185. EUPHORBIA APOCYNOIDES Kl.
Seemann 1096 (K).
186. EUPHORBIA MORISONIANA Kl.
Seemann 1652 (BM).*
190. SAPIUM MORITZIANUM Kl.
Seemann 1243 (BM).—Sterile.
191. OMPHALEA DIANDRA var. PANAMENSIS Kl.
Seemann 635 (BM).

192. ACALYPHA PANAMENSIS Kl.
Seemann s.n. (BM).
193. ACALYPHA SEEMANNI Kl.
Seemann 496 (BM).
194. ACALYPHA ALOPECUROIDEA Jacquin var. GLANDULIFERA Kl.
Seemann 297 (BM).
197. JATROPHA ELEGANS Kl.
Seemann 619 (BM).*
205. CAPERONIA PANAMENSIS Kl.
Seemann 189 (BM).
207. BARHAMIA PANAMENSIS Kl.
Seemann 201 (BM).*
208. CYCLOSTIGMA PANAMENSE Kl.
Seemann 1650 (BM).*
209. CYCLOSTIGMA DENTICULATUM Kl.
Seemann s.n. (BM).
219. CROTALARIA MAYPURENSIS HBK.
Seemann s.n. (BM).
224. TEPHROSIA NITENS Benth.
Seemann 1036 (BM).
226. LENNEA VIRIDIFLORA Seem.
Seemann 1189 (K).
230. STYLOSANTHES HUMILIS HBK.
Seeman 204 (BM).—This sheet may represent a mixed collection.
247. STENOLOBIUM BRACHYCARPUM Benth.
Seeman 215 (K).—Two sheets.
270. MACHAERIUM SEEMANNI Benth.
Seemann 1681 (BM).
273. LONCHOCARPUS VELUTINUS Benth.
Seemann 1183 (BM).*
275. PLATYMISCIUM POLYSTACHYUM Benth.
Seemann s.n. (BM).*
277. ORMOSIA PANAMENSIS Benth.
Seemann 1673 (BM).
298. BAUHINIA PARVIFOLIA Seem.
Seemann s.n. (BM).
316. CALLIANDRA SEEMANNI Benth.
Seemann 1X93 (BM).*
319. PITHECOLOBIUM GLOMERATUM Benth. var. SPICATUM Seem.
Seemann s.n. (BM).*
324. INGA TUBULIFERA Benth.
Seemann 1691 (BM).
328. INGA DARIENENSIS Seem.
Seemann 1050 (BM).
333. INGA PANAMENSIS Seem.
Seemann 407 (BM).*
336. INGA OERSTEDIANA Benth.
Seemann 1688 (BM).
Seemann X91 (BM).*
340. LICANIA ARBOREA Seem.
Cuming 1109 (BM).*
362. LOPEZIA PANICULATA Seem.
Seemann 1225 (BM).*
422. COUROUPITA ODORATISSIMA Seem.
Seemann s.n. (BM).
457. ERBLICHIA ODORATA Seem.
Seemann s.n. (K).
482. PENTAGONIA TINAJITA Seem.
Seemann 1595 (BM).—Two sheets.
483. PENTAGONIA PINNATIFIDA Seem.
Seemann 1019 (BM).
484. POSOQUERIA LATIFOLIA Roem. & Sch.
Seemann 1018 (BM).—Darien, Bay of Utria.
500. RONDELETIA PANAMENSIS De Cand.
Seemann s.n. (BM).—This may be a mixed collection judging by the geographical localities listed on the sheet: "Punta Gordo" and "New Granada (Prov. Bogota)."*
501. SIPANIA PALUSTRIS Seem.
Seemann 347 (BM).*
502. GONZALEA PANAMENSIS Pers.
Seemann 351 (BM).*
508. MALANEA ERECTA Seem.
Seemann s.n. (BM).*
525. CEPHAELIS PSYCHOTRIAEFOLIA Seem.
Seemann 482 (BM).*
539. VERNONIA SEEMANNIANA Steetz
Seemann 1589 (BM).*
550. TUBEROSTYLIS RHIZOPHORAE Steetz
Seemann 2801 or 2201 (BM).*
552. ADENOSTEMMA sp.
Seemann 1026 (BM).—Specimen in very poor condition.*
556. EUPATORIUM CONYZOIDES Vahl var. GLABRESCENS Steetz
Seemann 445 (BM).*
559. EUPATORIUM IRESINOIDES HBK. var. α VILLOSUM Steetz
Seemann 1024 (BM).*
559*. EUPATORIUM CRITONIOIDES Steetz
Seemann 1137 (BM).*
560. EUPATORIUM SCHIEDEANUM Schrader var. δ TOMENTOSUM Steetz
Seemann 1138 (BM).*
EUPATORIUM SCHIEDEANUM Schrader var. ε CAPITATUM Steetz
Seemann s.n. (BM).*
566. EUPATORIUM ELATUM Steetz
Seemann 448 (BM).*
573. CONYZA FLORIBUNDA HBK. var. β
Seemann 440 (BM).*
579. CLIBADIUM LEIOCARPUM Steetz
Seemann 1591 (BM).*
580. UNXIA DIGYNA Steetz
Seemann 46 (BM).*
584. WEDELIA CARNOSA Rich.
Seemann 42 (BM).
585. WEDELIA CARACASANA De Cand.
Seemann s.n. (BM).*
586. WEDELIA ACUMINATA De Cand.
Seemann s.n. (BM).
587. WEDELIA ACAPULCENSIS HBK.
Seemann 45 (BM).*
589. MELANANTHERA MICROPHYLLA Steetz
Seemann X52 (BM).

609. Senecio arborescens Steetz
Seemann 1134 (BM).*
619. Sophoclesia flaccida Seem.
Seemann 1080 (BM).
636. Strychnos panamensis Seem.
Seemann 1622 (BM).
637. Strychnos darienensis Seem.
Seemann s.n. (BM).—Two sheets, one sterile.
651. Schubertia tristis Seem.
Seemann 158 (BM).
664. Heianthus seemanni Griseb.
Seemann 1064 (BM).
665. Voyria simplex Griseb.
Seemann 186 (BM).
676. Ipomoea fistulosa Mart.
Seemann 177 (BM).*
Ipomoea—In "undetermined" folder
Seemann 175 (BM).
Seemann 352 (BM).
Seemann 2088 (BM).
685. Jacquemontia azurea Chois. var. alba Seem.
Seemann s.n. (BM).*
698. Solanum nutans Ruiz. et Pav. var. secundiflorum
Seemann 1072 (BM).*
Seemann 1X98 (BM).*
704. *Solanum mammosum* Linn.
Seemann s.n. (BM)*
709. Cyphomandra betacea Sendtn.
Seemann 1201 or *1207* (BM).
710. Pionandra allophylla Miers.
Seemann s.n. (BM).
718. Juanulloa panamensis Miers.
Seemann 1200 (BM).*
Seemann s.n. (BM).*
736. Lamourouxia scabra Benth.
Seemann 1175 (BM).
774. Tecoma guayacan Seem.
Seemann 558 (BM).
788. Scheeria panamensis Seem.
Seemann 235 (BM).
790. Columnea bilabiata Seem.
Seemann 1057 (BM).*
791. Columnea flaccida Seem.
Seemann 1163 (BM).*
792. Drymonia delphinioides Seem.
Seemann 1054 (BM).—Specimens in poor condition.
793. Alloplectus lanatus Seem.
Seemann s.n. (BM).
794. Alloplectus darienensis Seem.
Seemann 8501 (BM).
804. Hyptis vulcanica Seem.
Seemann 1603 (BM).
863. Persea veraguasensis Seem.
Seemann 1578 (BM).
872. Urera girardinioides Seem.
Seemann 494 (BM).
877. Pilea centradenioides Seem.
Seemann 1099 (BM).
882. Urostigma
Seemann 1574 (BM).
883. Urostigma liebmannianum Miq.
Seemann 497 (BM).
884. Urostigma sapidum Liebm.
Seemann 1157 (BM).
Seemann 1573 (BM).
885. Urostigma oerstedianum Miq.
Seemann 1158 (BM).
886. Olmedia armata Miq.
Seemann 1086 (K), *s.n.* (K, 2 sheets).
895. Peperomia quaternata Miq.
Seemann 1571 (BM).
904. Artanthe imperialis Miq.
Seemann 1065 (BM).*
905. Artanthe seemanniana Miq.
Seemann 1069 (BM).—Specimen fragmented.
907. Artanthe septuplinervia Miq.
Seemann 1066 (BM).
908. Artanthe calocoma Miq.
Seemann 1067 (BM).
909. Artanthe trinervia Miq.
Seemann 1217 (BM).*
910. Artanthe tricuspis Miq.
Seemann 1068 (BM).

Species treated in the "Supplement."

Hisingera nitida Hellen.
Seemann 1646 (BM).
Quercus seemannii Liebm.
Seemann 1228 (BM).
Quercus bumelioides Liebm.
Seemann s.n. (BM).

SOME COLLECTIONS DEPOSITED IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 1960–1969

SUSAN VERHOEK-WILLIAMS[1]

Prior to the 1950's a yearly list of the noteworthy collections received by the Missouri Botanical Garden Herbarium was included in the "Annual Report of the Director" published in the *Missouri Botanical Garden Bulletin*. The practice was discontinued in 1949. In the "Annual Report" for 1966 and in subsequent reports a few of the accessions for each year were cited. In order to complete the published record for the past decade and to expand the recent abbreviated listings in the *Bulletin*, the following list of accessions by the Missouri Botanical Garden Herbarium in the years 1960 through 1969 was compiled.

The data were taken primarily from the Herbarium's "Index to Collectors," a typewritten list of the names and collecting localities of collectors whose exsiccatae are housed in the Herbarium, and secondarily from the Herbarium exchange and purchase records. In the past the practice has been to include a name in the list of collectors only if a minimum number of specimens (approximately four), or type specimens, were received. This is simply a labor-saving device which avoids the tedious listing of miscellaneous student collections of two specimens sometimes received on exchange. The Herbarium exchange and purchase records, being kept according to institution rather than collector, rarely supplied additional information.

In gathering data for the list two criteria were used: (1) collecting dates between 1960 and 1969 and (2) recent entries in the "Index to Collectors" and the Herbarium exchange and purchase records. Some sets of collections made prior to 1960 have only lately been received by the Herbarium; they were identified by the personal recollection of the author, by handwritten entries in the typed collectors lists, or by a note in the exchange records.

An inherent problem in the compilation of any listing of collectors is misspelled names and incorrect or missing initials. An attempt was made to check the spellings of surnames and to obtain the correct initials using "Index Herbariorum Part I. The Herbaria of the World." Ed. 5. (Regnum Veg. 31. 1964), "Index Herbariorum Part II. Collectors A–D" (Regnum Veg. 2. 1954) and "Part II. Collectors E-H (Regnum Veg. 9. 1957), the American Society of Plant Taxonomists' "Index to Current Taxonomic Research, No. 6" (June, 1970, mimeographed), and the membership list of the International Association of Plant Taxonomists (Taxon 17: 749–796. 1968). Pertinent published floras were also consulted.

The greatest gap in the present list may be in the area of recent acquisitions of older specimens. My knowledge of the collections dates from 1966, and the "Index to Collectors" was retyped in that year. During retyping all of the lately-received-but-earlier-collected accessions were mingled into the same non-committal

[1]Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110. *Present address*: L. H. Bailey Hortorium, Cornell University, Ithaca, New York 14850.

type face with collections accessioned before 1960. The list is as complete as possible based in the available records but is not claimed to be definitive.

In the following compilation, the names of the collectors are grouped according to the major geographical areas of their collecting. For convenience all collections made in the U.S.S.R. are grouped together in the listing for Asia. Nations, especially the African ones, which have changed their names in the course of political restructuring are identified by the country name as it appears on the specimen labels rather than by the most recent designation.

For the sake of brevity, in cases where one botanist collected at various times each with a different person, as for example a professor with a succession of students, the listing is given under his name followed by the notation "with others" to denote a series of collections with each of a number of second collectors. For the accessions not collected between 1960 and 1969 the dates of collection are given.

NORTH AMERICA

ALDER, G. M.
Utah

ANDERSON, L. C.
Arizona, California, New Mexico

ANDERSON, L. E.
New York, North Carolina, Tennessee

ANDORFER, H.
Florida

ANWAY, J. C.
Arizona, Colorado, New Mexico, Utah

ARNOW, LOIS
Utah

ATWATER, W. G.
Florida, 1959

AUSTIN, D. F.
Kentucky

AVERY, G. N.
Florida

BANKS, D. J.
Alabama, Florida, Georgia

BARKER, W.
Kansas, North Dakota

BARKLEY, F.
Ohio

BARKLEY, T. & L. C. ANDERSON
New Mexico

BEATLEY, J. C.
Nevada

BLAISDEL, R. S.
Florida

BLUM, K.
Florida

BOLVIN, B.
Quebec

BOSTICK, V.
Nevada

BOWMAN, H. O.
Alabama

BREEDLOVE, D. I.
California

BREIL, D. A. & K. BLUM
Florida

BRINKER, R.
United States

BUCHANAN
Utah

CALDER, J. A. *et al.*
Queen Charlotte Islands

CHASE, V. H.
Illinois

CLEWELL, A. F.
Florida, Georgia

CODY, W. J. & L. VAN RENS
Canada

COOLEY, G. B.
Florida, 1957

CONARD, H. S.
Florida

COTTAM, W. P.
Utah

CRAIGHEAD, F. C.
Florida

CROAT, T. B.
Canada United States (Great Plains)

CROSSWHITE, F. S. & C. D. CROSSWHITE
Wisconsin

D'ARCY, W. G.
United States, chiefly Missouri

DAVIS, C. B.
Colorado

DEMAREE, D.
Southern United States

DEPOE, C. E.
Louisiana

DEWOLF, G. & PAMELA BRUNS
Massachusetts (Arnold Arboretum)

DICKSON, J. S.
Alaska
DRYSDALE
Western United States
ERLANSON, E. W.
University of Michigan Botanical Garden, 1922–1929
EVANS, A. M.
Florida
EVERS, R. A.
United States, chiefly Illinois
FARRER, M. J.
Utah
FLORES, C. & V. C. FLORES
Texas
FLOWERS, S.
Colorado, Utah
FREEMAN, J. D.
United States
GENTRY, H. & G. DAVIDSE
Western United States
___ & JENSON
Western and northwestern United States
GIBSON, A.
Massachusetts (Arnold Arboretum)
GILLIS, W. T.
Florida
GODFREY, R. K.
Florida, Georgia
___ & R. KRAL
Florida
GOODMAN, G. J.
Oklahoma
GRIFFIN, D.
Colorado, Florida, Tennessee
GUNN, C. R.
Iowa
GYADU, S. A.
Canada
HALL, H. H.
Colorado
HALL, M. T. *et al.*
Colorado, New Mexico
HARDHAM, C. B.
California
HARPER, K. T.
Utah
HARPER, R. M.
Florida, Georgia, Mississippi
HAVERBEKE, D. F. VAN
United States
HAWKSWORTH, F. G.
Arizona
___ & D. WIENS
Arizona, Colorado, New Mexico, Oregon
HEBERT, BRO. H.
Florida, Georgia, North Carolina
HEIMBERGER, C. & M. HEIMBERGER
Ontario
HEMPHILL
California
HENDERSON, N. C.
Central United States
HOLLAND, M.
Massachusetts (Arnold Arboretum)
HOLMGREN, N. H. & A. H. HOLMGREN
Utah
& J. L. REVEAL
California, Idaho, Nevada, Utah
HOWELL, J .T.
United States
& G. H. TRUE
Utah
HUDSON, C. & R. K. GODFREY
Florida
HUNTER, G. E.
Kentucky
ILTIS, H. *et al.*
Indiana, Wisconsin
ISELY, D.
Iowa, Oklahoma
JACKSON, C.
Florida, 1951
JONES, S. B., JR.
Florida, Georgia
KLICKOFF, L.
California, Utah
KRAL, R.
Eastern and southern United States
KURZ, H.
Southern United States, chiefly Florida
LAKELA, O.
Florida
LAZOR, R.
Florida
LEONARD, S. W. & A. E. RADFORD
North and South Carolina
LESCHKE, H.
California
LEWIS, W. H.
Southwestern Canada, United States
_____ *et al.*
Missouri (Missouri Botanical Garden)
LIGHTLE, P. C.
Arizona
LOGSTON, C. E.
Alaska
LONG, R. W.
Arkansas
___ WITH OTHERS
Florida
MACBRYDE, B.
Missouri
MCCART, W. L. & J. JUAREZ
Texas
MCDANIEL, S.
Southern United States
MACKEEVER, F. C.
Massachusetts
MACKENZIE, K. K.
Newfoundland, 1921

MAHLER, W. F.
United States
et al.
Montana, North Dakota, Wyoming
MEYER, F. G.
Northwestern United States
MILLER, MAUDE
Missouri, 1901
MOORE, J. W.
Minnesota, 1959
MORAN, R. V.
California
MOREY, D.
California, 1955
MUEHLENBACH, V. M.
Missouri
MURRELL, J. T.
Southeastern United States
NEILL, J. O.
Illinois, Missouri
NELSON, A. P.
California
NORRIS, R. A.
Florida
OLIVER, R. L.
Middle United States
OWNBEY, G. B.
United States
& J. MUGGLI
Minnesota
PARDUE, L. *et al.*
Florida
PARKS, J.
Florida
PEDERSEN, J. C.
Utah
PENN, G. H.
Louisiana
POLLARD, H. M.
California
PORTER, D. M.
Missouri
RAMSEY, G. W. *et al.*
North Carolina, Tennessee
RAY, J. D., JR.
Mississippi
REVEAL, J. L.
Western United States
WITH OTHERS
Western United States
RHOADES & HARVEY
Nevada
RICHARDSON, J.
Canada-United States (Great Plains)
& K. R. ROBERTSON
Midwestern United States
RIGGINS, RHONDA
Midwestern United States
ROBERT, H.
United States
ROBERTSON, K. R.
Kansas, Missouri
ROE, K. & F. ROE
Wisconsin
ROLLINS, R. C. *et al.*
Southeastern United States
RUBTZOFF, P.
California
RUNDE, R. H.
Missouri, Wisconsin
RUSSELL, N. H.
Virginia, 1958
SAMEJIMA, J. & K. SAMEJIMA
Southeastern United States
SEILER, G. E.
North Dakota
SHANBA, R. F. & F. H. NORRIS
Tennessee, 1947
SHINNERS, L. H.
Texas
SIEGLER, M.
Florida
SMALL, J. K.
Southeastern United States, 1924–1925
SMITH, A.
California
SMITH, R. R.
Florida
SORENSON, P.
Massachusetts (Arnold Arboretum)
SPENCER, W.
California
STEVENS, O. A.
North Dakota
STIMSON, W. R.
Florida
SUDA, Y.
Arkansas, Missouri
SULLIVAN, V. I.
Florida
THIERET, J. W.
Louisiana
THOMAS, R. D.
Louisiana, Mississippi
THORNE, R. F. & D. PROBST
California
& P. EVERETT
California
TWISSELMAN, E. C.
California
VENRICK, ELIZABETH
United States
VERHOEK-WILLIAMS, SUSAN & SHERI DAVIS
Missouri
VICKERY, R. K., JR.
Utah, 1959–1960
VOGNER, R. E.
Florida
WARD D. & E. WEST
Florida, 1959

& A. Will
Florida
Ward, R. L.
North Dakota
Weiler, J. H.
California, Oregon
Wemple, D. K.
Midwestern United States
Whitehouse, Eula
United States
Wiens, D.
Utah
Williams, S. F.
Michigan
Wooten, J. & V. Sullivan
Florida
Zaczkowski, N.
Montana, North Dakota, Wyoming

Mexico and Central America

Altig, R. *et al.*
Mexico
Atwood, J. T.
Nicaragua
Breedlove, D. E.
Guatemala
Bunting, G. S.
Mexico
Calderon, G. M.
Mexico
Carter, Annetta
Mexico
Cronquist, A.
Mexico
Duke, J. A.
Mexico
Dwyer, J. D. *et al.*
Belize, Costa Rica, Guatemala
Elias, T. S. *et al.*
El Salvador
Gentry, A.
Costa Rica
Godfrey, R. K.
Costa Rica
Hamblett, R. B.
Nicaragua
Hatheway, W. H.
Mexico
Johnson, C. D.
Guatemala, Mexico, Nicaragua
Koch, R. G.
Costa Rica
Laughlin, R. M.
Mexico
Lems, K.
Costa Rica
Lewis, W. H.
Mexico
MacDougal, T.
Mexico
Matuda, E.
Mexico
Maxwell, R. H.
Mexico
Molseed, E.
Mexico
Moore, A. D.
Nicaragua
Moran, R. V.
Mexico
Mori, S. *et al.*
Costa Rica, Mexico
Narvaez, G.
Nicaragua
Oliver, R. L. *et al.*
Mexico
Ozment, J. *et al.*
Mexico
Pennington, T. D. & J. Sarukhan K.
Mexico
Richards, E. L.
Mexico
Roe, K. *et al.*
Mexico
Rosas, M.
Mexico
Seymour, F. C.
Nicaragua
Skorepa, A.
Mexico
Stone, D. E.
Costa Rica
Ton, A. S.
Mexico
Ugent, D. *et al.*
Mexico
Webster, G. L. *et al.*
El Salvador, Honduras, Mexico
Wilbur, R. L. & D. E. Stone
Costa Rica
Williams, L. O. *et al.*
Honduras
Wilkes, H. B.
Guatemala, Mexico
Zelaya, H.
Nicaragua

PANAMA

AUSTIN, I. H.
AVILES, S.
1931
BARTLETT, H. H. & T. LASSER
1940
BLACKWELL, W. *et al.*
BLAISDEL, R. S.
BLUM, K. E.
BRISTAN, N.
BURCH, D. *et al.*
CASTILLO, J.
COHN, G. G.
CORREA A., MIREYA D.
et al.
WITH OTHERS
CROAT, T. B.
DRESSLER, R. L.
& MIREYA D., CORREA A.
& W. H. LEWIS
et al.
DUKE, J. A.
et al.
WITH OTHERS
DWYER, J. D.
et al.
WITH OTHERS
EBINGER, J.
ELIAS, T. S.
& SR. MARY VICTORIA HAYDEN
& J. H. KIRKBRIDE, JR.
FOSTER, R.
GODFREY, R. K.
HAYDEN, SR. MARY VICTORIA
HLADIK, ANNETTE
HOLDRIDGE, L. R.
HOWELL, J. H.
KILLIP, E. P.
1948
KIRKBRIDE J. H., JR.
KNIGHT, D.
KOZLOUSKY, D.
LALLATHIN, B. R.
LAZOR, R. L.
et al.
LEWIS, W. H.
et al.
WITH OTHERS
MCDANIEL, S.
MEANS, D. B. *et al.*
MORI, S.
NETTING, J. S.
NOWICKE, JOAN W. *et al.*
OLIVER, R. L.
& B. MACBRYDE
et al.
OPPENHEIMER, J.
PORTER, D. M. *et al.*
RIDGWAY, J. E. & R. SOLIS
SAWYER, J. L.
SEXTON, O.
SHATTUCK, O. E.
1931–1934
STARRY, D. E.
1931
STERN, W. L. *et al.*
TYSON, E. I.
et al.
WITH OTHERS
WEAVER, R. E., JR. & R. B. FOSTER
WENDEHAKE, CORINA
WESTON
WETMORE, R. H. & E. C. ABBE
1931–1932
WILLIS, BARBARA
1939
WILSON, C. L.
1931
WOOD, R. D.
WOODWORTH, R. H. & R. A. VESTAL
1932
ZETEK, J.
1937–1943

WEST INDIES

ANDERSON, W. R.
Jamaica
BALLIGNO, K. E.
Cuba
BURCH, D.
Dominica, Haiti
CHAMBERS, K. L.
West Indies
COOLEY, G. R.
West Indies
CRAIGHEAD, F. C. & J. POPENOE
Bahamas
CROSBY, M. R.
West Indies
DAWSON, E. Y.
Bahamas
DEWOLF, G. P.
Puerto Rico
DUKE, J. A.
Puerto Rico
GILLIS, W. B.
Bahamas
GONZALES, A.
Cuba, 1941
GRIFFIN, D.
Jamaica, Puerto Rico
HARTLEY, T. G.
Puerto Rico

HESPENHEIDE, H. A.
Jamaica
HOWARD, R. A.
Puerto Rico
LELLINGER, D. B.
West Indies
LEWIS, W. H.
Bahamas
MONTALVO, E. C.
Puerto Rico
STIMSON, W. R.
Puerto Rico, Virgin Islands
VOGNER, R. E.
Jamaica
VUILLEUMIER, BERYL
Jamaica
WAGNER, R.
Puerto Rico
WEAVER, R. E.
Jamaica
WEBSTER, G. L. *et al.*
Cuba, 1953
WILBUR, R. L.
Dominica
WOLLE, J.
Jamaica, 1847
WOODBURY, R.
Puerto Rico

SOUTH AMERICA

AGOSTINI, G.
Venezuela
ALBERTI, F. R.
Argentina
ARBO, M. M.
Argentina
ARISTEGUIETA, L. & G. AGOSTINI
Venezuela
AUSTIN, D. F.
Brazil
BELSHAW, C. M.
Peru, 1937
BISMARCK, K. VON
Peru
DODSON, C. H.
Peru
_____ & L. B. THIEN
Ecuador
DUARTE, A. P.
Brazil, 1946–1963
_____ *et al.*
Brazil, 1949
DUGAND, A.
Colombia
EISENDRATH, ERNA R.
Ecuador (Galápagos)
ESKUCHE, V.
Argentina
ESPINAL T. S.
Columbia
FERREYRA, R.
Peru, 1946–1967
FROES, R. L.
Brazil, 1942
GARCIA, C.
Ecuador
GILMARTIN, AMY J.
Ecuador
GRAZIELA
Brazil
GUIMARAES, O.
Brazil
GUSINDE, M.
Chile (Tierra del Fuego), 1921–1924
HAAS, H.
Brazil
HARLING, G.
Ecuador, 1959
HATHEWAY, W. H.
Colombia
HATSCHBACH, G.
Brazil, 1959–1969
HEINGER
Brazil
HUNT, D. R. & J. F. RAMOS
Brazil
HUTCHISON, P. C. *et al.*
Peru
ILTIS, H. H. *et al.*
Peru
IRWIN, H. S.
Surinam
_____ *et al.*
Brazil
JESUS, J. O. DE
Brazil
KING, R. M.
Brazil
KOCZICKI, C.
Brazil
KRAPOVICKAS, A.
Argentina, 1945–1946, 1964–1969; Brazil, Venezuela
_____ & C. L. CRISTOBAL
Argentina, Paraguay
LEMS, K.
Brazil
LOPEZ-PALACIOS & SEELKOPF
Venezuela
MACEDO
Brazil
MCKEE, H. S.
Venezuela
MAGALHAES, G. M.
Brazil
MAGUIRE, B.
Brazil, British Guiana, Surinam
_____ *et al.*

Brazil, British Guiana, Venezuela
WITH OTHERS
Brazil, British Guiana, Venezuela
MANDON, G.
Bolivia, 1858–1859, 1863
MARTIN, R. *et al.*
Peru
& C. LAU-CAM
Peru
MATHIAS, MILDRED E. & D. TAYLOR
Peru
MONTES, J. E.
Argentina, 1955–1958
MOODY, J. P.
British Guiana
PABST, G.
Brazil
PENNINGTON, T. D. & N. SILVA
Brazil
PIRES, J. M. *et al.*
Brazil
PRANCE, G. T. *et al.*
& N. T. SILVA
Brazil
RAGONESE, A. E.
Argentina
ROBERTSON, K. R. & D. F. AUSTIN
Guyana, Peru, Venezuela
ROBINSON
Colombia
SARAVIA, C.
Peru
SAUNDERS, S. E. G.
Peru
SCHULTES, R. *et al.*
Colombia
SILVA, N. T.
Brazil
SMITH, C. E.
Colombia, 1942
SMITH, L. B.
Brazil
et al.
Brazil
SODERSTROM, T.
Brazil
SOUKUP, J. & QUIRSE
Peru, 1948
STEINBACH, R. F.
Bolivia
STEYERMARK, J. A.
Bolivia, Venezuela
STRAW, R. M.
Peru
TILLETT, S. S. & C. L. TILLETT
British Guiana
UGENT, D. *et al.*
Bolivia
URIBE-URIBE, L.
Colombia, 1957–1968
VARGAS C., C.
Peru, 1958–1965
VEGA, F.
Brazil
VELEZ, PILAR DE
Ecuador
VILLAREAL, M.
Colombia, 1942–1943
VOGEL
Brazil
WEBER, W. A.
Ecuador (Galápagos)
WIGGINS, I. L.
Ecuador
& D. M. PORTER
Ecuador (Galápagos)
WOYTKOWSKI, F.
Peru
WRIGHT, J. K.
Peru
WURDACK, J. J.
Peru
et al.
Venezuela, 1955–1959

EUROPE

BOR, N. L.
Austria
BRUMMITT, R. K.
Great Britain
CANTELL, S.
Finland, 1937
DAY, F. W.
England
DEGENER, O. & ISA DEGENER
Europe
FREY, A. & L. FREY
Poland
GREEN, P. S.
Scotland
HAAKANA, A.
Finland
HAMMETT, K. R. W.
British Isles
HUBBARD, C. E.
British Isles
HUNT, D. R.
England
LAMOND, J. & P. WOOD
Scotland
MADALSKI, J. WITH OTHERS
Poland, 1939
MOCKETT, L. G.
British Isles
MUTCH, N.
England
PACYNA, A.
Poland

PIĘKOŚ, H.
Poland
SCHAUMAN, E.
Finland, 1950
SOULE, O.
Switzerland
SUISSE, O.
Italy
VÄNSKÄ, H.
Finland
VAUTIER, S.
Switzerland
WELCHE, M.
British Isles

ASIA

ABBAS, H. & F. A. BARKLEY
Iraq
AFANASSIEV, K.
U.S.S.R., 1932
AGNEW, A. D. Q.
Iraq
ANDREEV, V.
U.S.S.R., 1906
ARORA, C. M.
India
BARKLEY, F. A. & *et al.*
Iraq
BLOEMBERGER, S.
Indonesia, 1939
BOGDAN, V.
U.S.S.R., 1904
BUSCH, E. & N. BUSCH
U.S.S.R., 1927
CHAI, M.
Borneo
CHANG, L. M.
Formosa, 1950
CHEW, W. L. & E. J. H. CORNER
Malaya
CHUANG, C. C.
Taiwan
CORNER, E. J. H. & W. L. CHEW
Borneo
DERVIZ-SOKOLOVA, T.
U.S.S.R., 1958
DESOULAVI, N.
U.S.S.R., 1901, 1910
DIVAKAR, P.
India
DONK, M. A.
Indonesia, 1941
EIG, A.
Palestine, 1924
EVMENKOVA, I.
U.S.S.R.
FILATOVA, N.
U.S.S.R.
FORMAN, L. L.
Indonesia, 1956
GAMAJUNOVA, A.
U.S.S.R.
GIBOT, A.
Borneo
GOLOSKOKOV, V.
U.S.S.R., 1955, 1956, 1959, 1963
GRANT, M. L.
Iran
GROSS, K.
U.S.S.R., 1929
GUPTA, U.
India
GUSEV, J. & S. IKONNIKOV
U.S.S.R., 1958
GUYMER, D. A.
India
HUANG, T. C. & M. T. KAO
Taiwan
——— *et al.*
Taiwan
IRANI, N. A.
India, 1955, 1956
JACOBS, M.
Indonesia, 1939
JAIN, S. K.
India
JUZEPCZUK, S. WITH OTHERS
U.S.S.R., 1956–1958
KAO, M. T. & C. C. CHUANG
Taiwan
KAPOOR, S. L.
India
KAUL, K. N.
India, 1953, 1956
KAZAKEVICZ, L.
U.S.S.R., 1927
KINGDON-WARD, F.
India, Burma, 1949
KOLESNIKOVA, T. & N. TZERELEV
U.S.S.R.
KOSTERMANS, A. J. G. H.
Borneo
KUZNETZOV, I.
U.S.S.R., 1914
LEE, I. K.
Korea, 1957
LITVINOV, D.
U.S.S.R., 1909–1921
LUKANENKOVA, V.
U.S.S.R., 1958
MARCOWICZ, V.
U.S.S.R., 1916
MEIJER, W.
Borneo
MISRA, O. P.
India

MORDAK, H.
U.S.S.R.
MURRAY, E.
Turkey
NAFTOLSKY, N.
Palestine, 1931
NASAROV, M.
U.S.S.R., 1915
NEVSKI, S.
U.S.S.R., 1936
NICHOLSON, D. H.
Nepal
PANIGRAHI, G.
India
PAVLOV, V.
U.S.S.R., 1958
PLITMANN, U.
Palestine
POBEDIMOVA, E. & I. EVMENKOVA
U.S.S.R.
_ _ & V. GLADKOVA
U.S.S.R.
& V. GOLUBKOVA
U.S.S.R.
POLUNIN, O.
Kashmir, 1956
POPLAVSKAJA, H.
U.S.S.R., 1928
PROSAD, R.
India
RECHINGER, K. H. & F. RECHINGER
Iran, 1956–1959
ROLDUGIN, I.
U.S.S.R.
SANTAPAU, H.
India, 1953
SAUER, J. D.
India
SCHIRAEVSKY, I.
U.S.S.R., 1903
SCHISCHKIN, B. *et al.*
U.S.S.R., 1931
SKVORTSOV, A.
U.S.S.R., 1958
SOHMA, K.
Japan, 1956-1968
SOULE, O.
U.S.S.R.
SRIVASTAVA, J. G.
India, 1954
STEINBERG, E. & Z. VOROBJEVA
U.S.S.R., 1933
SUDA, Y.
Japan
SUTHERLAND, G. K.
Mesopotamia, 1916-1919
TATEOKA, T. & J. V. PANCHO
Philippines
TAVAKARI, S. C.
India, 1957, 1958
THEODOROV, A. *et al.*
U.S.S.R., 1948
TOLMATCHEVA, E.
U.S.S.R., 1958
TSENG, C. C.
Taiwan
TYRANOVETZ, V.
U.S.S.R., 1906
VASSILCZENKO, I. & L. VASSILJEVA
U.S.S.R.
VASSILJEVA, L.
U.S.S.R.
VETESCZAGIN, V.
U.S.S.R., 1927
VERMA, D. M.
India
WADHWA, B. M.
India
WAGH, S. K.
India, 1957, 1965
WIRAWAN, N.
Java
ZOHARY, M. *et al.*
Palestine, 1926, 1927

AFRICA

ACOCKS, J. P. H.
South Africa
ADAMES, P.
Liberia
ADAMSON, T.
Kenya, 1959, 1961
ADJANOHOUN, E.
Ivory Coast
ANDERSON, J. G.
South Africa
ANDRADA, E. C.
Mozambique, 1941
ANDREWS, F. W.
Sudan, 1939
ANGUS, A.
Zambia
ARCHBOLD
Tanzania
ARMITAGE, F. B.
Southern Rhodesia, 1957, 1959–1960
ARREY & H. SCHLIEBEN
South Africa
ASTLE, W. L.
Zambia
BAHADUR, B.
Africa
BAINBRIDGE, W. R.
Northern Rhodesia

BAKER, B. F.
Zambia
BARRETT, R. L.
Southern Rhodesia, 1956
BAYLISS, R. D. A.
South Africa
BEALE, W. P.
Gold Coast, 1929
BEESLEY, J. S. S.
Tanzania
BERNARDI, L.
Ivory Coast
BEST, E. R.
Northern Rhodesia
BIEGEL, H. M.
Rhodesia
BINGHAM, M. C.
Southern Rhodesia
BOALER, S. B.
Tanganyika
BOS, J. J.
South Africa
BOUGHEY, A. S.
Southern Rhodesia
BOULOS, I.
Egypt
BRETELER, F. J.
Cameroons
BREWER, J.
Southern Rhodesia
BULLOCK, A. A.
Zambia
BURGER, W.
Ethiopia
BUSHWORTH, J. E.
Rhodesia
CANNELL, I.
Rhodesia
CHAPMAN, J. D.
Nyassaland, 1954, 1956, 1958–1963
CHASE, N. C.
Mozambique, Nyassaland, Northern Rhodesia, Southern Rhodesia
CHEADLE, V.
South Africa
CLARK, D. H. M.
Southern Rhodesia
CLAYTON, D.
Kenya
CLEGHORN, W. B.
Southern Rhodesia, 1959–1962
CODD, L. E.
South Africa
COMPÈRE, P.
Congo
COMPTON, R. H.
South Africa
COOLEY, G. R. & L. KOFLER
Basutoland
CORBY, N. D. L.
Botswana
CORE, I.
Northern Rhodesia
CORREIA, M. F.
Mozambique
COTTRELL, M. L. J.
Zambia
DARAMOLA, B. O.
Nigeria
DARBYSHIRE, J. E.
Southern Rhodesia, 1959, 1960
DAVIES, R. M.
Southern Rhodesia, 1959–1961
DENNY, R. P.
Southern Rhodesia
DESCOINGS, B.
Congo
DEVENISH, N. J.
South Africa
DLAMM, B.
South Africa
DRUMMOND, R. B.
Southern Rhodesia
& R. O. B. RUTHERFORD-SMITH
Mozambique, Northern Rhodesia, Southern Rhodesia
EBBA, T.
Ethiopia
ECCLES
Nyassaland
EL-HADIDI, N.
Egypt
EMWIOGBON, J. A.
Nigeria
ENGLISH, N.
Rhodesia, 1958
FANSHAWE, D. B.
Northern Rhodesia-Zambia, 1959, 1962, 1964, 1965
FARRELL, J. A.
Southern Rhodesia
FAULKNER, H. G.
Tanganyika; Zanzibar, 1959–1963
FERREIRA, R. E. C.
Uganda
GAMBLE, J.
Mozambique
GARLEY, D. L.
Southern Rhodesia
GÉRARD, P.
Congo
GERMISHUIZEN, P. J.
South Africa
GILGES, W.
Zambia, 1955–1957
GILHAM, C. *et al.*
South Africa
GILLETT, J. B.
Kenya, Nigeria, South Africa, Zambia
GOMES E SOUSA, A. DE F.
Mozambique

Goodier, R.
Mozambique, Southern Rhodesia
& J. B. Phipps
Southern Rhodesia
Goodier, J. H.
Southern Rhodesia
Gordon, T. A. D.
Rhodesia
Greenway, P. J.
Kenya, South Africa, Tanganyika
Grosvenor, R. K.
Rhodesia
Grout, G.
Rhodesia, 1947
Guerra, (?M. S.) P.
Mozambique, 1931, 1933, 1935–1936
Hallé, N.
French Equatorial Africa
Hanssen, K.
Southern Rhodesia
Hasbrock
South Africa
Heberden, A. F.
Rhodesia
Hendrickx, F. L.
Congo
Hilliard, O. M.
Malawi
Hodgson, C. J.
Southern Rhodesia
Hodgson, L. M.
Rhodesia, 1956
Hough, R. J. de
Botswana
Humbles, J.
Tanzania
Huntley, B. J.
South Africa
Irvine, F. R.
West Africa, 1932–1937
Irwin, P. H.
Kenya
Jarman, P. J.
Rhodesia
Jeke, R. C.
Malawi
Jocot-Guillarmed, A.
South Africa
Jonker, P.
South Africa
Kafuli, D.
Zambia
Kennon, T. C. D.
Southern Rhodesia
Killick, D. J. B.
South Africa
Kirkham, N.
Rhodesia, 1951
Lambrecht, F. L. & C. Lambrecht
Botswana
Latilo, M.
Nigeria
Lauton, R. M.
Northern Rhodesia
Leach, L. C. with others
Northern Rhodesia, South Africa, Southern Rhodesia
Lefebure, J.
Algeria
Leeuwenberg, A. J. M.
Cameroon, Ivory Coast, Liberia
Leistner, O. A.
Bechuanaland, South Africa
et al.
South Africa
Lemos, F. L. de *et al.*
Southern Rhodesia
Lems, K.
Canary Islands
Lewalle, J.
Burundi
Lewis, W. H.
Angola, Ethiopia, Kenya, Rhodesia, South Africa, Swaziland, Tanganyika, Uganda
Liben, L.
Burundi, 1954
Lind, A. J. M.
Rhodesia
Linley, K.
Northern Rhodesia
Loveridge, J. P.
Northern Rhodesia, Southern Rhodesia
Luckhoff, H. A.
South Africa
Lusaka Natural History Club
Northern Rhodesia
McKay, A. D.
Botswana
Madgwick, Mrs. W.
South Africa
Marais, W.
South Africa, 1957, 1964
Marks, S. A.
Zambia
Marques, A.
Mozambique
Masterson, G. M.
Rhodesia
Mathias, Mildred E.
Tanganyika
Mauve, A. A.
South Africa
Mavi, S.
Rhodesia
Menavanza, I.
Congo
Mendes, E. J.
Angola, 1955–1960
Mendonça, F. A.
Mozambique, 1944, 1964

MEYER, F. G.
Ethiopia
MIDDLETON-STOKES, F. H.
Rhodesia
MILLS, A. P.
South Africa
MITCHELL, B. L.
Northern Rhodesia, Zambia
MITCHELL, D. S.
Northern Rhodesia
MITCHELL, J. C. G.
Southern Rhodesia
MOFFAT
Southern Rhodesia
MOOG, A. O. D.
South Africa
MOLL, E. J. & R. G. STREY
South Africa
MOONEY, H. F.
Ethiopia
MORRIS, D.
South Africa (Transvaal)
MORTON, J. K.
Sierra Leone
MOURA, A. R.
Mozambique
MSINKHU, J. B.
Malawi
MULLER, T.
Southern Rhodesia
MULLIN, L. J.
Rhodesia, 1951, 1954, 1964
MULLINS, J.
Southern Rhodesia
MUTIMUSHI, J. M.
Zambia
NGONI, J. F.
Rhodesia
NURSE, C. J.
Rhodesia
OATLEY, T. B.
South Africa
OKAFOR, J. C. & M. LATILO
Nigeria
OLDEMAN, R. A. A.
Ghana, Ivory Coast
ORPEN, F. I.
Rhodesia
PARDY, A. A.
Southern Rhodesia, 1928, 1931
PENN, E. G.
Southern Rhodesia, 1947
PERDUE, R. E. & S. P. KIBUWA
Kenya, Tanzania
PEREIRA, J. A. & M. GORREIA
Guinea
PHIPPS, J. B.
Southern Rhodesia
& D. VESEY-FITZGERALD
Northern Rhodesia, Tanganyika
PLOWES, D. C. H.
South Africa, Southern Rhodesia
POLE-EVANS, I. B.
South Africa
POLHILL, R. M. & S. PAULO
Tanganyika
POPE, G.
Rhodesia
PRINCE, S. D.
Zambia
RENSBERG, H. J. VAN
Northern Rhodesia, Zambia
REYNOLDS, B.
Northern Rhodesia, Southern Rhodesia
RICHARDS, MARY (MRS. H. M.)
Northern Rhodesia, Nyassaland, Tanganyika, Tanzania, Zambia
RICHARDSON, W. D.
Morocco
RISOPONLOS, S.
Congo, 1957
ROBINSON, E. A.
East Africa, Northern Rhodesia, Nyassaland, Southern Rhodesia, Tanganyika
ROSS, J. H.
South Africa
RUSHWORTH, J. E.
Rhodesia, 1958
RUTHERFORD-SMITH, R. O. B.
Rhodesia
SALUBENI, A. J.
Malawi
SANANE, M.
Zambia
SAUER, J. D.
Seychelles
SCHEEPERS, J. C.
South Africa, 1958–1967
SCHLIEBEN, H.
South Africa
SCHMIDT, A. A.
Congo
SEMSEI, S. R.
Tanganyika
SEWARD, B. L. S.
Rhodesia, 1951
SEYDEL, R.
South-West Africa
SHEPHERD, A. F.
Rhodesia
SIAME, W.
Zambia
SIMON, B. K.
Southern Rhodesia
—— WITH OTHERS
Rhodesia
SMARTT, J.
Northern Rhodesia
SOANE, C.
Southern Rhodesia, 1959, 1960

STEWART, E. A.
South Africa
STEWART, J.
Kenya
ST. JOHN (? H.)
Kenya, Tanganyika
STREY, R. G.
South Africa
STURDY, R. E.
Uganda
SYMOENS, J.-J.
Congo
SWINGLE, C. F.
Madagascar, 1928
TÄCKHOLM, VIVI
Egypt
TANNER, R.
Tanzania, 1959–1961
TAYLOR, H. C.
South Africa
THOM, J. E.
South Africa
THOMPSON, B. R.
Southern Rhodesia, 1951
THOMPSON, N. F.
South Africa
TORRE, A. R. & J. PAIVA
Mozambique
VAHRMEYER, J.
South Africa
VANDERBEN, D.
Congo, 1957
VERDCOURT, B.
Kenya
VESEY-FITZGERALD, D.
Bechuanaland, Malawi, Northern Rhodesia, Tanzania
VOORHOEVE, A. G.
Liberia
VUUREN, D. VON
South Africa
– & W. GIESS
South Africa
WAGEMANS, J.
Congo, 1951, 1957
WARD, C. J.
South Africa
WATMOUGH
Northern Rhodesia, 1959, 1960
WELLS, M. J.
South Africa
WERGER, M. J. A.
South Africa
WEST, O. B.
Northern Rhodesia; Southern Rhodesia, 1959–1968; Tanganyika
WILD, H.
Bechuanaland, South Africa, Southern Rhodesia
& R. B. DRUMMOND
Rhodesia
& L. C. LEACH
Mozambique
WILDE, J. J. F. F. DE
Ivory Coast
& A. J. M. LEEUWENBERG
Ivory Coast
& A. C. VOORHOEVE
Liberia
et al.
Cameroons
WILLIAMS, C. H.
Rhodesia
WINTER, B. DE
Bechuanaland, South Africa
& O. A. LEISTNER
South Africa, 1957
WORMALD, J. A.
Southern Rhodesia, 1951
WRIGHT, M. G.
Southern Rhodesia, 1947
YALALA, A. M.
Bechuanaland
YANSHAUVE, D. B.
Northern Rhodesia

OCEANIA

ABORN, R.
Hawaii
ANDERSON, J.
Australia
ASHBY, A. M.
Australia
BENNETT, E. M.
Australia
BURNS, A. C.
Australia
CLELAND, J. B.
Australia, 1955
CROSBY, M. R. & W. R. ANDERSON
Hawaii
DEGENER, O. *et al.*
Hawaii, Fiji
DONNER, N. N.
Australia
EICHLER, H.
Australia, 1956–1958
GARSTONE, P.
Australia
GEORGE, A. S.
Australia, 1957–1967
GREGORY, A. J.
Australia
HART, A. J.
Australia

HUTCHISON, P. C.
Hawaii
HUNT, D.
Australia
ISING, E. H.
Australia, 1957–1962
JACKSON, F. N.
Australia
LOTHIAN, T. R.
Australia, 1959, 1962
MCDONALD, H.
Australia, 1954–1960
NEWBY, K.
Australia
PFEIFFER, S. P.
Australia
ROBERTS, R. P.
Australia
ROGERSON, W.
Australia
ROHRLACH, K. D.
Australia, 1959, 1961
ROYCE, R. D.
Australia, 1959, 1966
SAFFREY, R. A.
Australia
SHARRAD, M. C.
Australia
SHOODE, R.
Austrtalia, 1957, 1958
SMITH, H. M.
Moorea
STEENBOHM, L.
Australia
& KELLY
Australia
ST. JOHN, H.
Australia
THOMPSON, J. A.
Australia
TINDALE, M. D.
Australia
WENT, F. W.
Australia, New Guinea
WHIBLEY, D. J.
Australia, 1957, 1959
WILSON, P. G.
Australia, 1958–1968
WIRAWAN, N.
Java

CHROMOSOME NUMBERS IN COMPOSITAE: COLOMBIAN AND VENEZUELAN SPECIES[1]

A. Michael Powell[2,3] and J. Cuatrecasas[4]

Abstract

Chromosome numbers are reported for 85 collections of Compositae, representing 26 genera and 68 species, from Colombia and Venezuela. Most of the counts are previously unreported, including four genera, *Blakiella* ($n = 9$), *Hinterhubera* ($n = 9$), *Oyedaea* ($n =$ ca. 28), and *Paragynoxys* ($n =$ ca. 40), and about 30 species of *Espeletia* (n = 19).

Chromosome counts for 85 collections of Colombian and Venezuelan Compositae are listed in Table 1. Bud material and the specimens were obtained by the junior author during his 1969 trips for collecting Compositae. The vials of buds were airmailed to the Department of Botany, Smithsonian Institution, and then relayed to Alpine, Texas, where counts were obtained by the senior author. Identifications were made by the junior author. Voucher specimens are deposited at US and COL or MER; duplicates will be distributed later. We are grateful to Robert M. King, Smithsonian Institution, for information regarding the genera of Eupatorieae.

Results and Discussion

Eupatorieae—The chromosome numbers listed for *Adenostemma* ($n = 10$), *Fleischmannia* (n 20), and *Lourteigia* ($n = 10$) correspond with previous records, although it should be noted that the species of *Fleischmannia* and *Lourteigia* were reported as *Eupatorium* (Cave, 1956–64; Powell & King, 1969). The count for *Critonia paezense* ($n = 10$) agrees with those obtained for five other species of this large genus, the others being reported as *Eupatorium* (R. M. King, personal communication).

Astereae—Counts listed for the species of *Baccharis* ($n = 9$) and *Conyza* ($n = 27$) are consistent with well established base numbers for the genera. The report for *Diplostephium glandulosum* ($n =$ ca. 9; Table 1) represents only the third species of this large genus for which chromosome numbers are available, with the other counts, for Peruvian species, also begin $n = 9$ (Turner, Powell & Cuatrecasas, 1967).

Chromosome counts for *Blakiella* ($n = 9$) and *Hinterhubera* ($n = 9$) are first reports. The type species of *Blakiella* (Table 1) was first published by Blake as *Podocoma*, a very different genus from southern South America and Australia (Cuatrecasas, 1969). A single species of *Podocoma* from Brazil, *P. hirsuta* ($n = 9$), has been reported by Coleman (1968). According to the thesis advanced by Solbrig *et al.* (1964), the new generic counts would seem to offer a small measure of support for the idea that $x = 9$ is the base number for Astereae.

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TABLE 1. Compositae of Colombia and Venezuela examined for chromosome number.

Species	*n* number	Locality and voucher
TRIBE EUPATORIEAE		
Adenostemma lavenia (L). Ktze.	10	COLOMBIA. VALLE: *Cuatrecasas & Patiño 27450.*
Critonia paezense (Hieron.) King & Robinson	10	COLOMBIA. VALLE: *Cuatrecasas, Patiño & Ramos 27506.*
Fleischmannia pycnocephala (Less.) King & Robinson	20	COLOMBIA. CAQUETA: *Cuatrecasas & Soderstrom 27198.*
Fleischmannia pycnocephala (Less.) King & Robinson	20	COLOMBIA. VALLE: *Cuatrecasas, Patiño & Ramos 27507.*
Lourteigia stoechadifolia (L. *f.*) King & Robinson	10	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27827.*
TRIBE ASTEREAE		
Baccharis prunifolia HBK	9[a]	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27081.*
Baccharis trinervis var. *rhexioides* (HBK) Baker	9	COLOMBIA. VALLE: *Cuatrecasas & Patiño 27344.*
Blakiella bartsiaefolia (Blake) Cuatr.	9	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28129.*
Conyza uliginosa (Benth.) Cuatr.	27	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27071.*
Diplostephium glandulosum Hieron.	ca. 9	COLOMBIA. CAUCA: *Cuatrecasas & Lehmann 27369.*
Hinterhubera imbricata Cuatr. & Arist.	9	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28022*
TRIBE INULEAE		
Gnaphalium graveolens HBK	ca. 14	COLOMBIA. NORTE DE SANTANDER: *Cuatrecasas & Rodríguez 27929.*
Gnaphalium graveolens HBK	14	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27870.*
TRIBE HELIANTHEAE		
Aldama dentata LaLlave & Lex.	17	VENEZUELA. MÉRIDA: *Cuatrecasas & Figueiras 28246.*
Ambrosia cumanensis HBK	18	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27855.*
Ambrosia cumanensis HBK	18	COLOMBIA. VALLE: *Cuatrecasas, Patiño & Caldas 27519.*
Aspilia tenella (HBK) Blake	ca. 17[b]	COLOMBIA. VALLE: *Cuatrecasas & Patiño 27354.*
Bidens rubifolia HBK	24	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27757.*
Calea caracasana HBK	24	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27841.*
Clibadium terebenthinaceum (Sw.) DC ssp. *colombiense* Cuatr.	16	COLOMBIA. VALLE: *Cuatrecasas, Espinal & Ramos 27601.*
Clibadium villosum Benth.	16	COLOMBIA. VALLE: *Cuatrecasas, Patiño & Ramos 27504.*
Espeletia arbelaezii Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27771.*
Espeletia arbelaezii Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27774.*
Espeletia atropurpurea A. C. Sm.	19	VENEZUELA. MERIDA: *Cuatrecasas, Figueiras & Marcano 28013*

TABLE 1. Continued.

Species	*n* number	Locality and voucher
Espeletia atropurpurea A. C. Sm.	19	VENEZUELA. TACHIRA: *Cuatrecasas, Figueiras & Marcano 28001.*
Espeletia brassicoidea Cuatr.	19	COLOMBIA. NORTE DE SANTANDER: *Cuatrecasas & Rodríguez 27916.*
Espeletia canescens A. C. Sm.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27900.*
Espeletia colombiana Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27812.*
Espeletia congestiflora Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27739.*
Espeletia conglomerata A. C. Sm.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27892*
Espeletia curialensis Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27790.*
Espeletia discoidea Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27775.*
Espeletia floccosa × *E. pannosa* hybrid?	ca. 19	VENEZUELA. TRUJILLO: *Cuatrecasas, Ruiz & Figueiras 28237.*
Espeletia figueirasii Cuatr.	19	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz, & Figueiras 28068.*
Espeletia frailejonota Arist.	19	VENEZUELA. TRUJILLO: *Cuatrecasas, Figueiras & Marcano 28173.*
Espeletia grandiflora H&B	19	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27094.*
Espeletia incana Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27729.*
Espeletia jahnii Standl.	19	VENEZUELA. TACHIRA: *Cuatrecasas, Figueiras & Marcano 27992.*
Espeletia lopezii Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27826.*
Espeletia muiska Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27776.*
Espeletia murilloi Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27743.*
Espeletia nemekenei Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27749.*
Espeletia neriifolia (HBK) Sch. Bip. var. *neriifolia*	19	VENEZUELA. DISTRITO FEDERAL: *Cuatrecasas, Aristeguieta & Velásquez 28244.*
Espeletia neriifolia var. *columbica* Cuatr.	19	VENEZUELA. MERIDA: *Cuatrecasas, Figueiras & Marcano 28019.*
Espeletia neriifolia (HBK) Sch. Bip. *ex* Wedd. var.	19	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28156.*
Espeletia neriifolia (HBK) Sch. Bip. *ex* Wedd. var.	ca. 19	VENEZUELA. TACHIRA: *Cuatrecasas, Figueiras & Marcano 27999.*
Espeletia neriifolia (HBK) Sch. Bip. *ex* Wedd. var.	19	VENEZUELA. TRUJILLO: *Cuatrecasas, Ruiz & Figueiras 28183.*
Espeletia petiolata Cuatr.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27876.*
Espeletia phaneractis (Blake) A. C. Sm. ssp. *boyacensis* Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27759.*
Espeletia phaneractis (Blake) A. C. Sm. ssp. *phaneractis*	19	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27070.*
Espeletia phaneractis × *E. corymbosa* hybrid.	19	COLOMBIA CUNDINAMARCA: *Cuatrecasas 27334.*

TABLE 1. Continued.

Species	*n* number	Locality and voucher
Espeletia pleiochasia Cuatr.	19	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27728.*
Espeletia santanderesis A. C. Sm.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27907.*
Espeletia sclerophylla Cuatr.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27868.*
Espeletia sericea Cuatr.	19	VENEZUELA. MERIDA: *Cuatrecasas, Figueiras & Marcano 28094.*
Espeletia standleyana A. C. Sm.	19	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27910.*
Espeletia weddellii Sch. Bip *ex* Wedd.	19	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28051.*
Espeletia weddellii Sch. Bip *ex* Wedd.	19	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28058.*
Espeletia sp.	19	VENEZUELA. MERIDA: *Cuatrecasas, Figueiras & Marcano 28096.*
Espeletia sp.	19	VENEZUELA. MERIDA: *Cuatrecasas, Figueiras & Marcano 28098.*
Espeletia sp.	19	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28142.*
Heliopsis buphtalmoides (Jacq.) Dunal	14	COLOMBIA. VALLE: *Cuatrecasas, Patiño & Ramos 27481.*
Montanoa lehmannii Hieron.	ca. 19[c]	COLOMBIA. TOLIMA: *Cuatrecasas & Echeverry 27717.*
Oyedaea verbesinoides DC.	ca. 28	VENEZUELA. DISTRITO FEDERAL: *Cuatrecasas, Aristeguieta & Velásquez 28245.*
Polymnia pyramidalis Triana	29	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Llano 27325.*
Polymnia pyramidalis Triana	29	COLOMBIA. TOLIMA: *Cuatrecasas & Echeverry 27621.*
TRIBE HELENIEAE		
Tagetes zypaquirensis HBK	12	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27847.*
TRIBE SENECIONEAE		
Neurolaena lobata (L.) R. Br.	11	COLOMBIA. VALLE: *Cuatrecasas & Patiño 27473.*
Paragynoxys meridana Cuatr.	ca. 40[d]	VENEZUELA. TACHIRA: *Cuatrecasas, Figueiras & Marcano 27995.*
Schistocarpha sinforosi Cuatr.	8	COLOMBIA. VALLE: *Cuatrecasas, Espinal & Ramos 27598.*
Senecio abietinus Willd. *ex* Wedd.	20	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27750.*
Senecio andicola Turcz	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27294.*
Senecio canescens var. *boyacensis* Cuatr.	20	COLOMBIA. BOYACA: *Cuatrecasas & Rodríguez 27814.*
Senecio formosus HBK	ca. 40	COLOMBIA. VALLE: *Cuatrecasas, Espinal & Ramos 27556.*
Senecio formosus HBK	ca. 40	COLOMBIA. SANTANDER: *Cuatrecasas & Rodríguez 27904.*
Senecio ledifolius (HBK) DC.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27086.*
Senecio ledifolius (HBK) DC.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27291.*

TABLE 1. Continued.

Species	*n* number	Locality and voucher
Senecio longipenicillatus Sandw.	20	VENEZUELA. MERIDA: *Cuatrecasas, Ruiz & Figueiras 28026.*
Senecio nitidus (HBK) DC.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27292.*
Senecio pulchellus (HBK) DC.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas 27079.*
Senecio pulchellus (HBK) DC.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27300.*
Senecio silvascandens Cuatr.	20	COLOMBIA. TOLIMA: *Cuatrecasas & Echeverry 27632.*
Senecio trichopus (Benth.) Greenm.	20	COLOMBIA. CAUCA: *Cuatrecasas & Lehmann 27383.*
Senecio vaccinioides (HBK) Sch. Bip. *ex* Wedd.	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27299.*
Senecio vacinioides × *S. ledifolius* hybrid	20	COLOMBIA. CUNDINAMARCA: *Cuatrecasas & Heisser 27301.*

[a] Actually recorded as $n = 9$ II + 2 B chromosomes.
[b] Actually recorded as $n = 16$ or 17 II.
[c] Actually recorded as $n = 19$ II ± 1.
[d] Actually recorded as $n = 38$–40 II.

Inuleae—The previously unreported *Gnaphalium graveolens* ($n = 14$) has the same chromosome number as several other South American species of the genus.

Heliantheae—The chromosome numbers obtained for *Aldama dentata* ($n = 17$), *Ambrosia cumanensis* ($n = 18$), *Bidens rubifolia* ($n = 24$), *Calea caracasana* ($n = 24$), *Clibadium villosum* ($n = 16$), and *C. terebenthinaceum* ($n = 16$) agree with previous reports (Turner, Powell & King, 1962; Powell & King, 1969). The count for *Aspilia tenella* ($n =$ ca. 17) differs from earlier reports for two other species of the genus (*A. helianthoides*, $n = 14$; *A. rudis*, $2n = 28$; Ornduff, 1967), but the approximate nature of our count should be emphasized because the determination was made from "sticky" meiotic configurations. However, Turner and Lewis (1965) have found $n = 34 \pm 2$ for *A. africana*, and although the latter count is also approximate, it is reasonable to suggest that more than one base number may exist in this large genus distributed from Mexico to Brazil and Africa.

The counts for about 30 species and two interspecific hybrids of *Espeletia* (Table 1) are all $n = 19$. This would seem sufficient to establish a consistent base number of $x = 19$ for the genus. The counts are all first reports except for *E. grandiflora* which has been recorded earlier along with three additional species also $n = 19$ (Powell & King, 1969). *Espeletia* thus remains chromosomally distinct from the related *Polymnia* ($x = 14$, 15, 16, 17; Cave, 1956–64; Ornduff, 1967). *Polymnia pyramidalis* ($n = 29$; Table 1) corresponds with previous reports for this species (Powell & King, 1969).

Heliopsis buphtalmoides (n = 14) has been recorded by several workers, and the count for *Montanoa lehmannii* (n = ca. 19) agrees with that reported previously for two other species of the genus (Turner & Johnston, 1961; Turner & Flyr, 1966).

The approximate count (Table 1) for *Oyedaea verbesinoides* (n = ca. 28), a first generic report, lends tentative support for the supposed close relationship between *Oyedaea, Zexmenia* (x = 10, 11, 14), *Aspilia* (x = 14, 17?), and *Wedelia* (x = 11, 12, 15). The chromosomal variability exhibited by the above genera, including a host of polyploids reported for *Wedelia,* suggests that cytological investigations will contribute significantly toward the eventual resolution of relationships among the taxa.

Helenieae—Tagetes zypaquirensis with n = 12 is consistent with one earlier report (Powell & King, 1969).

Senecioneae—The chromosome numbers for *Neurolaena lobtata* (n = 11) and *Schistocarpha sinforosi* (n = 8) are previously well documented (Powell & King, 1969). The count for *Paragynoxys meridana* (n = ca. 40) is an initial report for the genus. *Paragynoxys* is related to *Gynoxys* which also has been reported as n = ca. 40 (Turner *et al.*, 1967).

Counts for the eleven species of *Senecio* (n = 20, ca. 40) augment the already huge list of species of this genus for which chromosome numbers are known. Eight of these species, *S. abietinus* (n = 20), *S. andicola* (n = 20), *S. canescens* (n = 20), *S. longipenicillatus* (n = 20), *S. nitidus* (n = 20), *S. silvascandens* (n = 20), *S. trichopus* (n = 20), and *S. vaccinioides* (n = 20) are previously unreported. All these are woody shrubs or trees except *S. longipenicillatus,* a subshrub. It can be noted that the counts obtained for the herbaceous polymorphic species *S. formosus* (Table 1) are n = ca. 40, while one earlier record for this taxon was n = ca. 20 (Powell & King, 1969).

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NEW COMBINATIONS IN THE SOLANEAE (SOLANACEAE) AND COMMENTS REGARDING THE TAXONOMIC STATUS OF *LEUCOPHYSALIS*[1]

JOHN E. AVERETT[2]

ABSTRACT

New combinations are made for four species previously included in *Chamaesaracha*.

During the course of a revisionary study of *Chamaesaracha*, several species were encountered that are better treated in other genera. With the removal of these species, *Chamaesaracha* becomes a natural, closely knit genus of seven species restricted to the desert regions of the southwestern United States and adjacent northern Mexico. New combinations for these species are as follows:

Saracha potosina (Rob. & Greenm.) Averett, *comb. nov.*

Chamaesaracha potosina Rob. & Greenm., Amer. Jour. Sci. 50: 161. 1895. [MEXICO. SAN LUIS POTOSI: Tamasopo Canyon, Nov. 1880, *Pringle 3654* (VT, holotype).]

The fruiting calyx of this species is rotate and expanding under the berry like that of other species of *Saracha* and unlike those of *Chamaesaracha*.

Physalis sinensis (Hemsl.) Averett, *comb. nov.*

Chamaesaracha sinensis Hemsl., Jour. Linn. Soc. Bot. 26: 174. 1890. [CHINA. Hupeh, *Henry 2902* (K, holotype, not seen; NY, isotype).]

This species has an inflated, ribbed fruiting calyx which encloses the berry and therefore belongs with *Physalis*.

Leucophysalis heterophylla (Hemsl.) Averett, *comb. nov.*

Chamaesaracha heterophylla Hemsl., Jour. Linn. Soc. Bot. 26: 176. 1890. [CHINA. Hupeh, *Henry 6207* (K, holotype, not seen; GH, NY, isotypes).]

This species is transferred to *Leucophysalis* on the basis of its floral and fruiting characters.

Leucophysalis nana (Gray) Averett, *comb. nov.*

Saracha nana Gray, Proc. Amer. Acad. Arts 10: 62. 1874. [CALIFORNIA. Sierra Nevadas, 1868–69, *Kellogg & Harford 719* (GH, hololectotype; US, isolectotype).]

Chamaesaracha nana (Gray) Gray, Bot. California 1: 540. 1876.

Although the fruiting calyx of this species does not always exceed the berry in length, it is transferred to *Leucophysalis*. Like *L. grandiflora* the berry is fleshy

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and the placenta extends the entire length of the berry with seeds attached all along the placenta. In *Chamaesaracha* the berry is dry, and the placenta is mostly basal. The species of *Chamaesaracha* are extremely uniform in the placental character, and the differences exhibited by *L. grandiflora* are significant. In addition, flavonoid data (Averett & Mabry, 1970) suggest an affinity between *L. grandiflora* and *L. nana.* The flavonoid profiles of the two species are identical except for the absence of one compound from the complement in *L. nana.*

Some comment on *Leucophysalis* is in order since its taxonomic status may be somewhat confused. *Leucophysalis* was established as a monotypic genus by Rydberg (1896) to accommodate *L. grandiflora,* formerly included in *Physalis* by Hooker (1840), Fernald (1949: 82–83) compared *L. grandiflora* with certain Asian species of what he considered to be *Chamaesaracha,* and as a consequence transferred it to the latter genus. However, unbeknownst to Fernald, Makino (1914: 20–22) had removed the Japanese species from *Chamaesaracha* placing them in his newly established genus *Physaliastrum.* If the relationship Fernald suggested exists, and indeed, it may, the species in question still do not belong with *Chamaesaracha.* Rather, they should all be treated as *Leucophysalis.* Investigations are currently underway to bring additional evidence to bear on the question.

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NOTES

CHROMOSOME NUMBERS OF PHANEROGAMS. 4.[1]

Chromosome numbers of phanerogams are reported below together with voucher data and herbaria where collections are deposited. Unless indicated otherwise the chromosome records are based on the study of one plant. Haploid counts are from pollen mother cells, and diploid counts are from root tips unless otherwise indicated. An asterisk (*) indicates that one or more permanent slides are available at the Missouri Botanical Garden Herbarium.

The authors responsible for counts are listed alphabetically. Citation should have the form: Doe, J. 1970. *In* Chromosome numbers of phanerogams. 4. Ann. Missouri Bot. Gard. 57:

Counts by Walter H. Lewis and Royce L. Oliver, Missouri Botanical Garden.[2]

All counts based on seedlings except *Ipomoea aquatica* which is based on a stem cutting.

Apocynaceae

Himatanthus bracteata (A. DC.) Woodson. 2n = 18. Guyana. About 20 mi. S of Georgetown, 1 mi. N of Atkinson Field Airport, *Robertson & Austin 290* (MO, NY).

Bignoniaceae

Saldanhaea seemanniana O. Kuntze.—Erroneously reported as 2n = 18 in "Chromosome Numbers of Phanerogams. 3" (Ann. Missouri Bot. Gard. 56: 472. 1969). The correct number is 2n = 40.

Convolvulaceae

Ipomoea aquatica Forsk. 2n = 30. Guyana. Livestock farm, Central Agriculture Station, *Robertson & Austin* 329 (MO).

Leguminosae

Erythrina chiriquensis Krukoff. 2n = 42. Panama. Chiriqui: Altitude 6000 feet, Butcher *s.n.* (MO).

Erythrina coralloides DC. 2n = 42. Mexico. Michoacan: Between Jiquilpan and Quiroga, *Krukoff 1970–132* (NY).

Erythrina costariensis M. Micheli. 2n = 42. Costa Rica. san jose: Near San Isidoro General, *Krukoff 1969–152* (NY).

Erythrina edulis Triana. 2n = 42. Colombia. cundinamarca: Seeds

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[1]The previous number in this series appeared in Ann. Missouri Bot. Gard. 56: 471–475. 1969.

[2]Supported by National Science Foundation grant GB-5042.

collected by *Garcia-Barriga* and sent as *Krukoff 20112* (MO).

Erythrina goldmanii Standley. 2n = 42. MEXICO. CHIAPAS: Between Tapachula and Tanala, *Krukoff 1970–72* (NY).

Erythrina huehuetenangensis Krukoff & Barneby. 2n = 42. GUATEMALA. HUEHUETENANGO: Munic. Berillas, Finca San Isidoro, *Krukoff 1969–274* (NY).

Erythrina lanata Rose. 2n = 42. MEXICO. SINALOA: *McVaugh 15782* (MICH). Cultivated at Missouri Botanical Garden (66–83–2).

Erythrina oliviae Krukoff. 2n = 42. MEXICO. PUEBLA: Km 230/231 of Mexico-Oaxaca highway, bank of dry stream, *Krukoff 1970–108* (NY).

Erythrina standleyana Krukoff. 2n = 42. MEXICO. CAMPECHE: Between Escarcega and Chetumal, *Krukoff 1970–54* (NY).

Erythrina steyermarkii Krukoff & Barneby. 2n = 42. COSTA RICA. ALAJUELA: San Carlos, Finca Los Ensayos, *Krukoff 1969–145* (NY).

Erythrina tajumulcensis Krukoff & Barneby. 2n = 42. GUATEMALA. SAN MARCOS: Near Aldea Feria, *Krukoff 1969–249* (NY).

Identification of all species of *Erythrina* were made by Dr. B. A. Krukoff whose assistance is very much appreciated.

MELIACEAE

Cedrela angustifolia Sesse & Moc. *ex* DC. 2n = 54. PANAMA. PANAMA: Cerro Campana, three-fourths of way to summit from Pan American Highway, *Dwyer et al. 4860* (MO, NY, UC).

RUBIACEAE

Oldenlandia cf. *crassifolia* DC. 2n = 34. TAIWAN. ILAN COUNTY: Tali. Seeds from Dr. T. C. Huang, progeny *Lewis 6797* (MO, SING).—Determined by Dr. H. Keng, University of Singapore. Doubtfully distinct from *Hedyotis*—the specific epithet is however preoccupied in that genus.

Counts by BRUCE MACBRYDE, Pontificia Universidad Catolica del Ecuador and Missouri Botanical Garden.

MALPIGHIACEAE

Galphimia angustifolia Bentham. n = 12. TEXAS. TRAVIS COUNTY: 15 mi. NW of Austin, Kretschmar sect., Austin Project, Texas Systems of Natural Labs., *Lynch 710* (MO).—Plant potted and growth resumed at Missouri Botanical Garden.

Galphimia gracilis Bartling. n = 12. FLORIDA. SARASOTA COUNTY: Sarasota, cultivated at 1315 S. Charlotte, *MacBryde & Herrera-MacBryde 63* (MO).—Seed grown at Missouri Botanical Garden (68–98–1).

Counts by KENNETH R. ROBERTSON, Missouri Botanical Garden.

CONVOLVULACEAE

Jacquemontia havanensis (Jacquin) Urban. 2n = 20.* BAHAMA ISLANDS. GRAND BAHAMA: Dead Man's Reef, *Lewis 7097* (2 plants). ELEUTHERA: The

Current, *Lewis 7409;* SE tip of Island, *Lewis 7446.*—Plants grown from seed at Missouri Botanical Garden; vouchers in MO.

Jacquemontia pentantha (Jacquin) G. Don. n = 9.* MEXICO. QUINTANA ROO: Cozumel Island, vicinity of San Miguel de Cozumel, *Lewis 6853.*—Plant grown from seed at Missouri Botanical Garden; voucher in MO.

Jacquemontia tamnifolia (L.) Grisebach. 2n = 18.* GUYANA: Vicinity of Georgetown, 1 mi. N of Atkinson Field Airport, *Robertson & Austin 285.*—Plant grown from seed at Missouri Botanical Garden; voucher in MO.

Counts by JOHN C. SEMPLE, Missouri Botanical Garden.

COMBRETACEAE

Conocarpus erecta L. 2n = 24. BAHAMA ISLANDS, GREAT EXUMA: Seed collected by Dr. Norton H. Nickerson from Hummingbird (Jewfish) Cay.—Grown at Missouri Botanical Garden, voucher *Semple 493* (MO). Six plants counted.

MALPIGHIACEAE

Galphimia angustifolia Benth. 2n = 20. TEXAS, JIM WELLS COUNTY: About 4 mi. NW of Orange Grove (collection by Fred B. Jones).—Potted and regrown at Missouri Botanical Garden, voucher *B. MacBryde 72* (MO).

Heteropteris angustifolia Griseb. 2n = 34. CALIFORNIA. From Los Angeles State & County Arboretum.—Seed grown at Missouri Botanical Garden (69–18–4), voucher *B. MacBryde 73* (MO). Two plants counted.

Lophanthera lactescens Ducke. 2n = 12. BRAZIL, PARA: Belém, Horto Museu Geoldi, seed collected by P. B. Calvalcante.—Grown at Missouri Botanical Garden. *Austin 4236* (MO) may be considered the voucher, since it is from the same tree in Belém. Two plants counted.

POLLEN GERMINATION IN *MONOTROPA*

During a current study to determine plastid presence and morphology in the achlorophyllous, saprophytic plant, *Monotropa uniflora* L., we also examined sections of anthers for the presence of pollen. The specimens were prepared for electron microscopy according to conventional methods. Sections of anthers revealed both intrasporal development as well as occasional intramicrosporangial development of the microspore.

Figure 1 shows an oblique section of the developing male gametophyte. Both the tube (vegetative) and generative cells can be easily seen. The tube cell cytoplasm contains profiles which have been interpreted as plastids (P) and mitochondria (M) on the basis of plastid and mitochondrial structure in leaf transections. The tube cell also contains numerous ribosomes, both small and large vesicles, dictyosomes (D), and profiles of endoplasmic reticulum. The tube

FIGURE 1.—Oblique section of male gametophyte of *Monotropa uniflora*, × 8750. See text for explanation of letters.

nucleus (TN) contains dense masses of DNA near the nuclear membrane. The various layers of the microspore wall are clearly evident: the slightly tectate ektexine (EK), the endexine (EN), and the intine (I).

The generative cell is separated from the tube cell by plasma membranes. The organelles appear reduced both in number and development. The ribosomes are numerous and occasional profiles of rough endoplasmic reticulum are evident.

The generative nucleus (GN) is very dense with clumps of DNA material appearing both next to the nuclear envelope and transecting the nucleoplasm.

The observations reported here for the germinating pollen tube of *Monotropa* are similar to those reported by Jensen, Fisher, and Ashton (Planta 81: 206–228. 1968) in *Gossypium* and by Larsen (Amer. Jour. Bot. 52: 139–154. 1965) in *Parkinsonia, Hymenocallis, Hippeastrum,* and *Ranunculus*. Pollen tubes of *Monotropa* show intrasporangial development and presence of plastids. No lipid storage products are evident.—*John E. Ridgway, Department of Biology, Washington University, St. Louis, Missouri 63130.*

A NEW SPECIES OF *LECYTHIS* FROM PANAMA

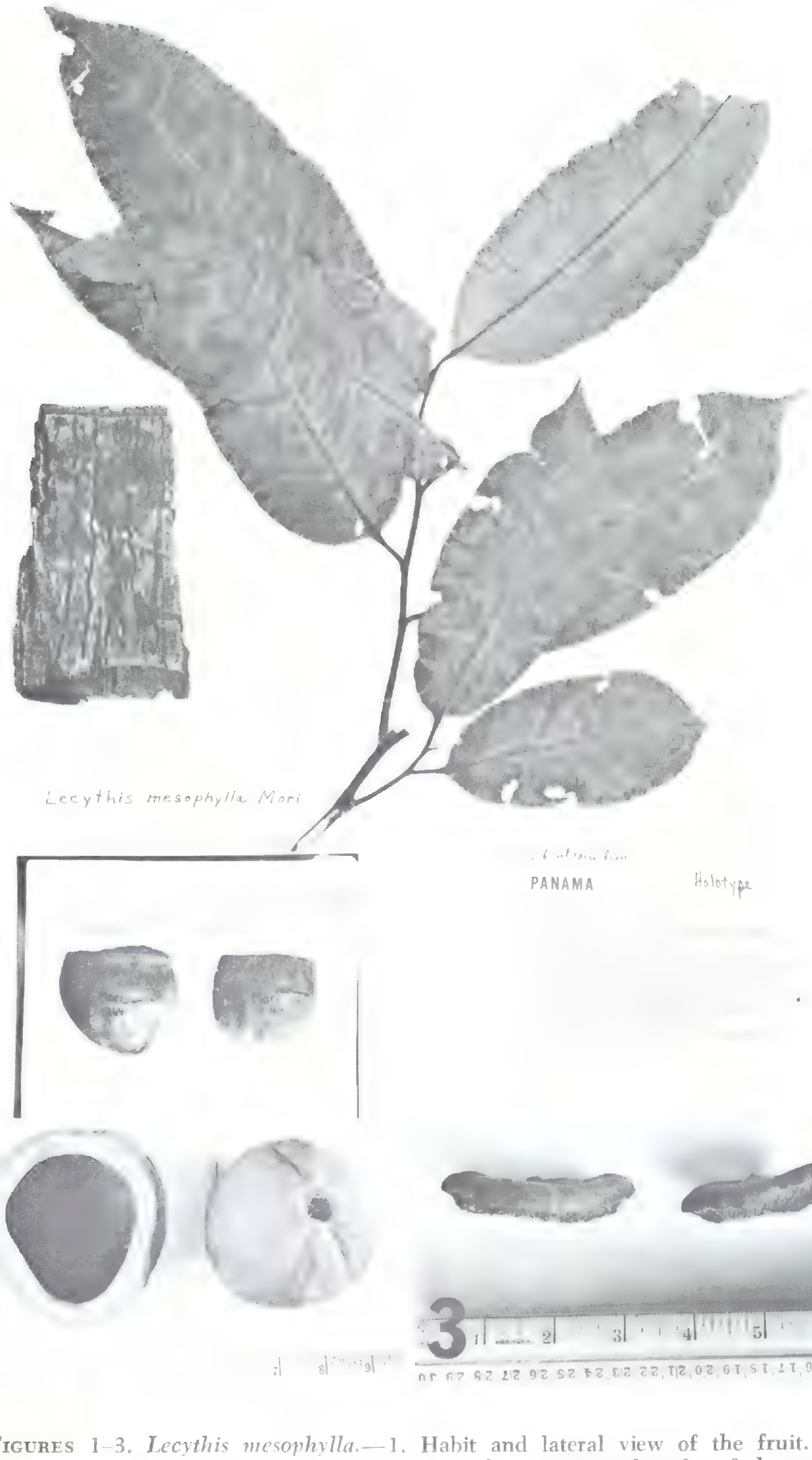
Lecythis mesophylla Mori, sp. nov.

Type: PANAMA. DARIEN: N slope of Cerro Pirre, ca. 1300 m, *Mori 364* (WIS, holotype; F, MO, NY, UC, US, isotypes.)

Arbor usque ad 40 m alta, 27 m ad ramum primum, capitulo sparso, trunco recto, 85 cm diametro; cortex badius, fissuris horizontalibus et longitudinalibus, parvis partibus emittentibus; lignum succosum cremeum, 5–10 cm latum; lignum centrale rubrum. *Folia* lanceolata ad elliptica, coriacea, glabra, 12.5–17.5 cm longa, 4.7–6.7 cm lata; apices acuminati; bases obtusae vel rotundatae; margines crispi, crenulati vel integri, minutis (0.5–1.0 mm longis), cicatricibus brunneis; nervatura reticulata, costa prominenti et 10–15 venis lateralibus, 1 cm intra marginem secedentibus; petioli 1.1–1.6 cm longi, laminis leviter decurrentibus usque ad ½ longitudinem petioli. *Fructus* globosi, lignosi, 8.2–10.4 cm longi (sine operculo), 8.6–11.0 cm lati; pericarpium laevigatum, 0.6–1.2 cm crassum; zona supra 6 cicatrices sepalorum 2.7–4.5 cm lata; zona infra 6 cicatrices sepalorum 4.2–7.1 cm lata, 4–6 sulcis longitudinalibus; bases fructuum obliquae; cicatrix pedicelli 1.1–1.9 cm lata; orificium operculi 5.7–8.3 cm latum, triangulatum in forma; operculum planum, irregularis ad marginem, umbone spinifro.

Tree to 40 m, 27 m to the first limb, bole straight, 85 cm DBH, crown sparse; bark light brown, with longitudinal and horizontal fissures, shedding in small flakes; sapwood cream colored, 5–10 cm wide; heartwood red. *Leaves* lanceolate to elliptic, coriaceous, glabrous, 12.5–17.7 cm long and 4.7–6.7 cm broad, the apices acuminate, the bases obtuse to rounded; margins crisped, crenulate to entire; minute (0.5–1.0 mm long) brown scars left by caducous hairs along the margins, midrib prominent; petioles 1.1–1.6 cm long; leaf blades narrowly decurrent to about ½ the petiole length. *Fruits* globose, woody, 8.2–10.4 cm long (without operculum), 8.6–11.5 cm wide; pericarp smooth, 6–12 mm thick; supracalycine zone 2.7–4.5 cm wide; infracalycine zone 4.2–7.1 cm wide; the bases of the fruit lopsided, often with 4–6 longitudinal grooves arising in the infracalycine zone and ending at the pedicel scar; pedicel scar 1.1–1.9 cm wide; 6 linear sepal scars protruding slightly from the fruit surface; operculum flat with a small spine-tipped umbo, edge of the operculum irregular.

On November 15, 1967 Narciso Bristan of El Real, Darien, guided me to the Cerro Pirre campsite of Dr. James Duke. This temporary collecting station, consisting only of a palm-thatched lean-to, is located three hours by boat and another six hours by foot south of El Real. Where the trail begins to ascend the slopes of Cerro Pirre small-fruited trees of *Lecythis mesophylla* are common—about 20 individuals were counted before reaching the campsite. The leaves are intermediate in size between the smaller ones of *L. costaricensis* and the larger ones of *L. tuyrana* and *L. elata*. The fruits are much smaller than those of *L. costaricensis* and can be distinguished from the fruits of *L. tuyrana* and *L. elata* by their distinctive spine-shaped umbo and the longitudinally grooved infracalycine



FIGURES 1–3. *Lecythis mesophylla*.—1. Habit and lateral view of the fruit. 2. Top and bottom views of the fruit. –3. Opercula, note the spine-tipped umbo of the operculum on the right.

zone. The fruits of *L. minor* of Colombia are smaller, and the operculum lacks the spine-tipped umbo of *L. mesophylla*. None of the species descriptions listed by Knuth (Lecythidaceae. *In* A. Engler, "Das Pflanzenreich." 105(2): 1–146. 1939) fit this entity.—*Scott Mori, University of Wisconsin Herbarium, Madison.* Present address: *Department of Botany and Zoology, The University of Wisconsin Center System, Wood County Campus, Marshfield, Wisconsin 54449.*

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